

3 Taxonomy, Identification and Principal Species

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3.1 Introduction

3.1.1 History

‘On closer examination the root was found to be covered with excrescences varying from the size of a small pin’s head to that of a little Bean or Nutmeg.’ This observation, from one of the first accounts of root-knot nematodes on plants, was made by Berkeley (1855), an eminent Victorian scientist, on publishing his discovery of galls produced by nematodes on the roots of cucumbers growing in a garden frame at Nuneham, England. Miles Joseph Berkeley FRS (1803–1889), an ordained minister, expert draughtsman and pioneering zoologist, plant pathologist and mycologist (he authored over 6000 species), went on to describe the symptoms thus: ‘The tubercles were of a dirty cream colour, nearly globose, obscurely furfuraceous, and in almost every case were developed on one side of the root...’. Berkeley (Fig. 3.1) noted the enormous development of the vascular tissues

within the galls and recorded the presence of ‘Vibrio’:

It appeared that these cysts were regular membranous sacs, exactly resembling the sporangia of Truffles, and filled with a multitude of minute elliptic or slightly cymbiform eggs, averaging not more than 1/250th of an inch in length with a breadth of 1/600th. In many of these the nucleus already showed the form of a Vibrio, folded up once or twice, and several of the animals were free, though still of small size, having escaped from the eggs by a little circular aperture at one extremity.

Berkeley illustrated his account with two rather nice drawings showing the symptoms on the roots and a section through one of the galls (Fig. 3.2).

The occurrence of galls on plant roots was also recorded in some detail by Licopoli (1875), who described tubercles on the roots of *Sempervivum tectorum* L. and other Crassulaceae in Italy. Licopoli dissected the tubercles and recorded the presence of ‘miriadi di Anguillole simili a quelle che talvolta rinvengonsi nel frutto del

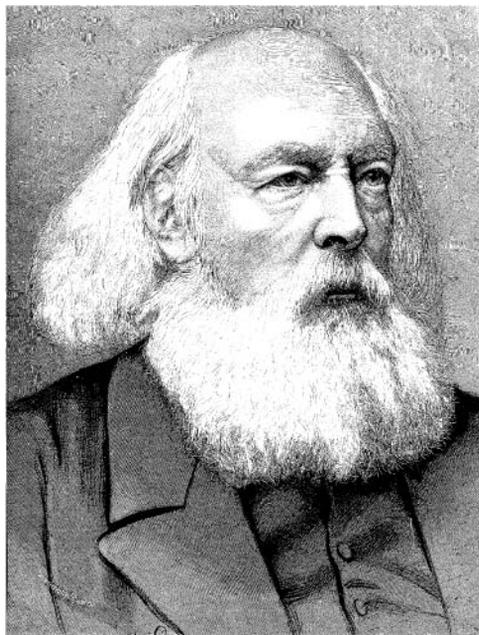


Fig. 3.1. The Rev. Miles Joseph Berkeley FRS (1803–1889). Berkeley, a pioneering mycologist and plant pathologist, was the first to publish a paper on root-knot nematodes.

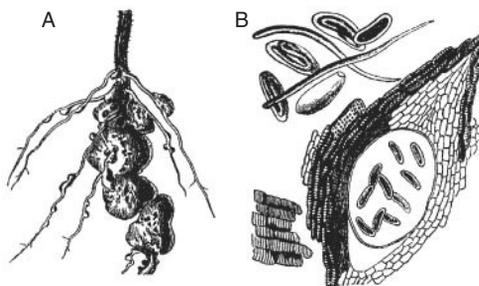


Fig. 3.2. The first illustration of root-knot nematodes on plant roots. A: galled roots; B: section through gall, showing nematodes and eggs. After Berkeley (1855).

formento e del fico non ben maturato' [‘myriads of little anguillole, like those sometimes found in the fruit of wheat and in not well-matured fig.’]. Similarly, Jobert (1878) described galls on the roots of coffee trees from Rio de Janeiro state, Brazil, and referred to the presence in the galls of eggs containing juveniles.

None of these early workers actually named the nematodes that they found in the galls, this being left to a French botanist, Maxime Cornu, who referred to the nematodes from galls on sain-

foin as *Anguillula marioni* Cornu, 1879. Cornu (1843–1901) did a thorough study of the phenomenon, comparing the root-knot galls with the nodules on leguminous plants and those formed by *Phylloxera vastatrix* on vine roots (Cornu, 1879). Carl Müller (1884) was the first to illustrate a perineal pattern while describing root-knot nematodes, which he erroneously referred to as *Heterodera radicolica* (Greeff, 1872) Müller 1884, confusing nematodes previously described as *Anguillula radicolica*¹ by Greeff (1872) with the root-knot nematodes that he, Müller, had found in the same host. This inadvertent error would have unfortunate repercussions as Cobb (1924) subsequently used Greeff’s name as the type of his new genus, *Caconema*.

The Dutch botanist Melchior Treub (1851–1910), who worked in the Dutch East Indies from 1880 to 1909, described the next species of root-knot nematode when he proposed *Heterodera javanica* Treub, 1885. This nematode was isolated from the roots of sugarcane from the Buitenzorg Botanical Gardens in Java, Indonesia (Treub, 1885). The description was rather short on detail and lacked figures.

Although two species of root-knot nematode had so far been named, the actual genus name of *Meloidogyne* was not proposed until 1887 when Göldi (Fig. 3.3) described *Meloidogyne exigua* Göldi, 1887 from galls on coffee roots in Rio de Janeiro state, Brazil. Émil August Göldi was born in Switzerland on 28 August 1859 and emigrated to Brazil in 1880, where he worked as a zoologist at the Museu Nacional do Rio de Janeiro, and later at the Museu Paraense, an institution that was renamed in his honour as the Museu Paraense Emilio Goeldi in 1902. In Brazil, he spelled his name as Emilio Augusto Goeldi, hence the two surname variants seen in the literature. Göldi returned to Switzerland in 1905, dying in Zurich on 5 July 1917 at the age of 58. In his proposal of the genus *Meloidogyne*, Göldi (1887) provided a full-page plate of line drawings of the nematodes that he had found, but, although the figures clearly show that it was a root-knot nematode, there are few meaningful data by today’s standards to establish its precise identity (Fig. 3.4).

In the literature, the publication date of Göldi’s description of *M. exigua* is variously cited as 1887 or 1892. While it is clear that Volume VIII of *Archivos do Museu Nacional*, the journal in which the

¹ Now known as *Subanguina radicolica*.



Fig. 3.3. Emílio Augusto Göldi (1859–1917), the proposer of the genus *Meloidogyne*. Image from http://pt.wikipedia.org/wiki/Imagem:Goeldi_Emilio_Augusto_1859-1917.jpg. Accessed September 2007.

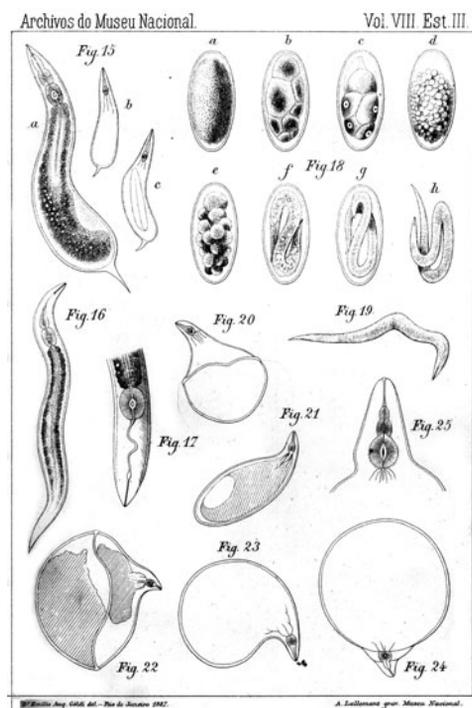


Fig. 3.4. Plate of original line drawings of *Meloidogyne exigua*. Although lacking much of the detail required for species diagnosis, the tail spike characteristic of a developing root-knot nematode can be clearly seen in Fig. 15. After Göldi (1887), courtesy of *Archivos do Museu Nacional, Rio de Janeiro*.

description was printed, was actually published in 1892 (see Lordello, 1951; Wouts and Sher, 1971; Fortuner, 1984; Karssen, 2002, for example), an advance copy or preprint of the article exists, clearly imprinted with 1887 as the date of publication and with different pagination to the 1892 version (Göldi, 1887, 1892). A preprint may be defined as ‘a work published, with its own specified date of publication (imprint date), in advance of its later reissue as part of a collective or cumulative work. Preprints may be published works for the purposes of zoological nomenclature’ (see Glossary and Article 21.8 in International Commission on Zoological Nomenclature, 1999).

Whitehead (1968) referred to this ‘advance copy’ in his bibliography, and accordingly used the earlier year of 1887 as the date of publication for the genus and type species. Other authors using the earlier date include Chitwood (1949), who, however, cited the 1892-published journal as the reference source, Sasser (1960), Franklin (1957, 1965a, 1976) and Jepson (1987), although most later authors, including Siddiqi (1986, 2000), Eisenback (1997), Karssen and van Hoenselaar (1998), Karssen (2002) and Karssen and Moens (2006), use the 1892 date.

We have examined an archive copy of the preprint from the United States Department of Agriculture (USDA) National Agricultural Library at Beltsville, Maryland. The title page clearly carries the imprint date of ‘1887’² (compare this with the journal volume title page, which has the imprint 1892) and is paginated from 1 to 121 with an additional index page followed by four plates of figures and a map entitled ‘Zona affectada pela Molestia do Cafeeiro, Agosto, 1887’. A typed note (authorship unknown) taped to the inside cover of the preprint declares that ‘The material [in the 1892 paper] is the same as in this preprint, 1887.’ An additional note indicates that Göldi published essentially the same information, although in a ‘somewhat condensed’ form, in 1888 (Göldi, 1888). The 1888 paper was published in the March issue of *Revista Agricola* and includes the four plates and map found in the 1887 and 1892 publications. On p. 42 of this article, Göldi discusses the proposal of the new name ‘*Meloidogyne exigua*’ and, in a footnote, cites the new genus name as ‘*Meloidogyne* nov. gen. Göldi (1887)’, and

² Thereby distinguishing it from a separate.

provides an etymology and diagnosis of the genus. Göldi also published an article entitled 'Biologische Miscellen aus Brasilien. VII. Der Kaffeemotode Brasiliens (*Meloidogyne exigua* G.)' in 1889 (Göldi, 1889). In this article he discusses '*Meloidogyne exigua* G.', provides some morphological data of the various stages and compares it with *Heterodera*. It is clear, therefore, that the description of the genus and type species was validly published before the 1892 date commonly cited, the earlier preprint of 1887 satisfying the requirements of Article 21.8 of the Code for a nomenclatural act, and thus qualifying as the actual publication date for the genus and binomen. In this chapter, therefore, we accept 1887 as the actual date of publication for the genus and type species.

Shortly after Göldi's proposal of the genus *Meloidogyne*, Neal (1889), clearly unaware of the former publication, proposed the gall-forming nematode, *Anguillula arenaria* Neal, 1889. Neal produced a comprehensive, highly detailed and nicely illustrated paper on the root galls of plants, including radishes, and peach, fig and orange trees, in Florida, USA (Fig. 3.5; Plate 1). The quality of this paper easily surpassed all that preceded it, notwithstanding the fact that Neal was almost certainly dealing with more than one species of root-knot nematode (see Chitwood, 1949). Neal referred to reports of this root-knot disease being recognized as far back as 'the earliest settlement of the South Atlantic and Gulf states by white people' and stated 'In 1869 I found the root-knot prevalent over Florida, and learned from old residents that as far back as 1805 it had been known'.

In the same year that Neal published his work on nematode galls in Florida, Atkinson (1889) found 'giant cells' in cross-sections of root-knot nematode-infected roots, although he interpreted these as dead females rather than nutritional devices. Atkinson gave an account of the life history of these nematodes, which he referred to as '*Heterodera radicicola* (Greeff) Müller', thereby repeating Müller's mistaken identity of some 5 years previously (Müller, 1884).

Other reports of root-knot nematodes include those of Cobb (1890), from New South Wales, Australia, and Laverne (1901a,b). The latter report is of some interest, as Gaston Laverne described *Anguillula vialae* Laverne, 1901 from the roots of vines in Chile; the recent discovery of *Meloidogyne ethiopica* Whitehead, 1968 from vines

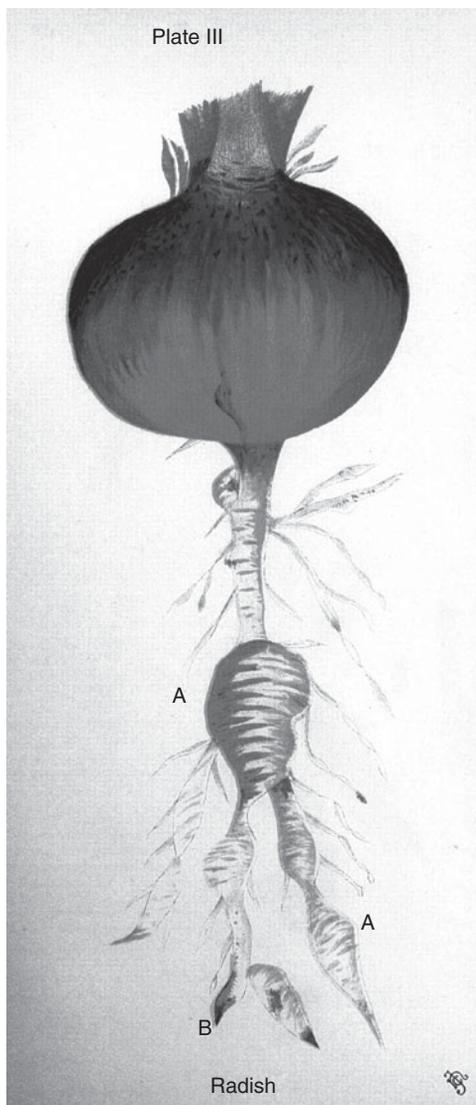


Fig. 3.5. Root galling on radish caused by *Anguillula* [= *Meloidogyne*] *arenaria*. After Neal (1889), courtesy of USDA.

and kiwi fruit in Chile and other South American countries has led to the suggestion that Laverne's record may actually refer to *M. ethiopica* (Carneiro *et al.*, 2007), although proof is lacking.

In the first decade of the 20th century, Kati Marciniowski (1909) differentiated in detail the differences between cyst and root-knot nematodes. She recognized only one species of root-knot nematode, however, synonymizing all the

other nominal species (including *arenaria*, *exigua* and *javanica*) to *H. radiculicola*.

One of the more controversial aspects of taxonomy in this genus occurred in 1919 when Kofoid and White, working in the USA, described a new species of oxyurid from 'Man'. They had isolated numerous viable nematode eggs from the faeces of troops stationed in Texas and other military units from Oklahoma, New Mexico and Arizona, yet these eggs did not correspond in dimension to any of the helminths known to be parasitic in humans. They named their species *Oxyuris incognita* Kofoid & White, 1919, the specific epithet reflecting their uncertainty as to the status of this 'new nematode infection of Man'. As is usual for helminth identification, the dimensions of the eggs were recorded, length varying from 68 to 133 μm and diameter from 33 to 43 μm . The large range in length may indicate that more than one nematode species was represented, although the generic identity of these eggs is uncertain.

Sandground (1923), commenting on the occurrence of similar eggs found in the course of hookworm campaigns in the USA and other countries, stated:

The fact that the eggs were found sporadically in the stools and that their occurrence was especially noticeable in the summer, a period when vegetable salads are a significant article in the diet, made it seem feasible to the writer that they originated in plant parasitic nematodes and were introduced with the food.

His research indicated that when bean roots infected by root-knot nematodes (which he referred to as *H. radiculicola*) were ingested by humans the eggs could pass through the body and be recovered from the stools, the eggs being of similar appearance to those previously attributed to *O. incognita*. He therefore concluded that the eggs recorded by Kofoid and White (1919) were the product of a root-knot nematode rather than being laid by an unknown helminth as previously surmized.

Cobb (1924), recognizing that there were differences between cyst-forming and root-knot nematodes, proposed the genus *Caconema* Cobb, 1924 to contain the latter. The type species of this new genus was *H. radiculicola*, itself a confused appellation because of the misidentification dating back to Müller (1884). Tom Goodey (1932) did not accept Cobb's proposal of *Caconema* as he regarded root-

knot and cyst-forming nematodes as congeneric. Goodey (1932) regarded *A. marioni* Cornu, 1879, the oldest name applied to root-knot nematodes, as belonging to the genus *Heterodera*, a combination that had previously been proposed by Marcinowski (1909). What is now known as *Meloidogyne marioni* is currently regarded as a *species inquirenda* due to a lack of informative morphological detail.

Although Nagakura (1930) published an extensive study on root-knot nematodes, differentiating them in numerous ways from cyst nematodes and making observations on their morphology and life cycle, he still referred to them as *H. radiculicola*.

The root-knot nematodes received their first major revision when Chitwood (1949) published a defining overview of the group. Chitwood resurrected the genus *Meloidogyne* as proposed by Göldi (1887) with *M. exigua* as type, even though there was no type material available of this species and the description itself was too poor to enable species identification (yet good enough to establish the genus). Chitwood placed three other species in the genus, making the new combinations *M. incognita*, *M. javanica* and *M. arenaria*. The identity of at least *M. incognita* and *M. javanica* was at best equivocal due to their inadequate original descriptions, *O. incognita* being based solely on a series of rather variable egg dimensions that may well have represented more than one species, while '*Heterodera javanica*' did not even figure in the description by Treub (1885). Although these actions established the fundamental framework for root-knot nematode taxonomy, some authors, notably Gillard (1961) and Whitehead (1968), criticized the resurrection of a genus name perhaps best left forgotten and the recognition of old species names whose true identity was highly dubious – not to mention the fact that Chitwood, perhaps mischievously, cited the type host of *M. incognita* as 'Man', on the basis that the eggs were first isolated from the stools of troops! Chitwood, however, made it very clear that his objective was to establish firmly the older names and thereby stabilize the existing nomenclature. Accordingly he provided redescriptions of the four old names (*arenaria*, *exigua*, *incognita*, *javanica*), based on new material that was often allocated in a somewhat arbitrary way, e.g. his description of *M. exigua*, originally described from Brazil, was based on nematodes from coffee plants in the New York

Botanical Garden, while his description of *M. incognita* used material from carrots in Texas, on the basis that this was the commonest root-knot in the state and therefore the species that the troops, from whom Kofoid and White (1919) had obtained the eggs of *O. incognita*, would probably have ingested. Chitwood also established the use of perineal patterns as a useful diagnostic aid and described *Meloidogyne hapla* Chitwood, 1949. Whatever the veracity of the arguments concerning the validity of the genus and the status of its species, there is no denying that Chitwood produced a seminal paper that clearly demarcated the differences between root-knot and cyst-forming nematodes, and simultaneously laid the foundations for future research.

Sledge and Golden (1964) proposed the genus *Hypsoperine* Sledge & Golden, 1964 for species of *Meloidogyne* where the mature female was characterized by a thicker cuticle and an elevated, cone-like posterior region. The history of this genus has been somewhat chequered, with many authors (e.g. Whitehead, 1968; Hirschmann, 1985; Jepson, 1987) regarding it as a junior synonym of *Meloidogyne*, while Siddiqi (1986) not only recognized it as a valid genus but split it into two subgenera, *Hypsoperine* (*Hypsoperine*) and *Hypsoperine* (*Spartonema*). However, in the second edition of his *magnum opus*, Siddiqi (2000) synonymized *Hypsoperine* (*Hypsoperine*) under *Meloidogyne*, but raised the former subgenus *Spartonema* to genus rank. Plantard *et al.* (2007), on the basis of 18S rDNA sequences, refuted the generic status of *Spartonema*, a decision which is accepted herein.

3.1.2 Major reference sources

The major reference sources for root-knot nematode taxonomy start with the monograph by Chitwood (1949). Although some of his nomenclatural decisions were considered to be at fault by other workers, the paper has rightly become the benchmark for all subsequent work. Intraspecific variability, long the bugbear of root-knot nematode diagnostics, was studied by a number of authors, including Allen (1952) and Dropkin (1953). The importance of the perineal pattern in identification was stressed by Sasser (1954), Taylor *et al.* (1955) and Triantaphyllou and Sasser (1960), among others. Mention must also be made of the monograph by Whitehead (1968), a neat piece of research that drew together

much useful information and in which he proposed four new species and recognized 23 as valid. The introduction of that paper is both cogent and comprehensive, and covers the history of the group in far more detail than has been given in the current chapter. Franklin (1971) reviewed the genus and included some 32 species, whilst Esser *et al.* (1976) provided a compendium to facilitate identification of 32 species. In a later work, Franklin (1979) again reviewed the genus, recognizing 36 valid species. Five years later, this total had risen to 54 species and two subspecies (Hirschmann, 1985). Other major reference sources include the monograph by Lamberti and Taylor (1979), the compendium by Hewlett and Tarjan (1983), the two-volume treatise edited by Sasser and Carter (1985) and Barker *et al.* (1985), the insightful, abundantly illustrated monograph by Jepson (1987) and the comprehensive and highly practical root-knot nematode taxonomic database compiled on CD-ROM by Eisenback (1997). The latest monographs are by Karssen and van Hoenselaar (1998) and Karssen (2002), both of which cover the European species of the genus, and Karssen and Moens (2006), where 89 valid species are listed. Karssen (2002) provides an interesting and detailed account of the history of the group.

3.1.3 Rate of species descriptions

Between 1880 and 1960, only eight valid species had been described, many of the intervening decades passing with none or only a single new species being named. No doubt this was in part a reflection of the conserved morphology of this fascinating group of plant parasites, the mature females, for example, showing few useful characters apart from those of the anterior region (labial annulation, stylet form and excretory pore position) and the perineal pattern around the vulva–anus region. Another consideration is the fact that the genus is predominantly tropical or subtropical in distribution, areas where there were few nematologists to take an interest in taxonomy. In the five decades since 1959, the pace of species description has been spectacular, with 18 being described in the 1960s, six in the 1970s, 30 in the 1980s, 22 in the 1990s and 12 since the millennium. By June 2009 there were 97 valid species in the genus.

3.1.4 Recent advances in characterization

The perineal pattern was initially thought to be rather more useful as a diagnostic character than eventually proved to be the case, intraspecific variation and a large increase in the number of nominal species taking their toll on its utility, particularly for the inexperienced eye. Although various characters from the male and second-stage juvenile (J2) were pressed into service, it was not until the advent of isozyme and molecular methodologies that a new window on species concept within the group opened, with the result that species otherwise camouflaged by intraspecific variability of the perineal pattern (the *incognita*-type pattern is particularly common, for example) can now be targeted with greater precision than hitherto.

3.2 Systematic Position

Because of certain similarities in morphology and biology, root-knot nematodes and cyst-forming nematodes have often been thought to be closely related. As a consequence, in many systematic schemes both groups were often placed in a single family or subfamily, the Heteroderidae or Heteroderinae, respectively, closely related to the hoplolaemids. A growing suspicion indicated, however, that the two groups had probably evolved separately and had achieved their similarities via the process of convergent evolution. According to this view, the root-knot nematodes justify their own family or subfamily and are closer to the pratylenchids than to the hoplolaemids.

Root-knot nematodes were first placed in their own subfamily when Skarbilovich (1959) proposed the Meloidogyninae, thereby emphasizing the differences between root-knot and cyst-forming nematodes. The Meloidogyninae was originally regarded as a subfamily under the Heteroderidae, although subsequent workers (e.g. Jepson, 1987; Siddiqi, 1986, 2000; Karsen, 2002) have recognized it at family level, as a sister taxon to either the cyst-forming nematodes or, latterly, the pratylenchids.

The advent of molecular methodologies has facilitated a better understanding of the phylogeny of the Nematoda. As a result, the morphology-based systematics schemes have now been largely replaced by hierarchies based on molecular phylogeny (see De Ley and Blaxter, 2002, 2004). In their attempt

to unify the systematics, De Ley and Blaxter introduced the infraorder. The consequence of this action is automatically to cascade a reduction in rank to all subsidiary taxa so that, for example, the former ranks of superfamily, family and subfamily become family, subfamily and tribe, respectively. In this account we follow the scheme outlined in De Ley and Blaxter (2004), with the result that the former family Meloidogynidae is reduced in rank to a subfamily within the Hoplolaemidae. By adopting this scheme, taxa previously regarded as subfamilies should either be reduced in rank to tribe or discarded – we have followed the latter course.

3.3 Subfamily and Genus Diagnosis

The following diagnoses of the family and genus are based on those of Siddiqi (2000) but have been updated to reflect the fact that we reject *Hypsoperine*, including the subgenus *Spartonema*, as valid taxa. *Hypsoperine* and *Spartonema* were also rejected as valid genera by Plantard *et al.* (2007).

Subfamily Meloidogyninae Skarbilovich, 1959

- = Meloidogynini Skarbilovich, 1959
- = Meloidoderellinae Husain, 1976
- = Meloidoderellini Husain, 1976

Diagnosis: Hoplolaemidae. Root-gall inciting, female feeding inciting multinucleate nurse cells. Marked sexual dimorphism. Cuticle striated. Lateral fields bearing four or five incisures. Labial region low, with one to four annules. Under SEM (scanning electron microscopy), female labial disc dorso-ventrally elongate, dumb-bell-shaped with oral opening a small, round pore surrounded by six inner labial pits (sensilla). Framework moderately sclerotized, hexaradiate; lateral sectors equal to, or wider than, submedian sectors. Stylet moderately strong, male stylet longer and more robust than that of female. Orifice of dorsal pharyngeal gland located just posterior to stylet base. Median pharyngeal bulb oval or round, with large refractive thickenings. Pharyngeal glands elongate, extending over intestine mostly ventrally but also laterally; subventrals asymmetrical, extending past dorsal gland, SVN (subventral gland nucleus) always posterior to DN (dorsal gland nucleus). Excretory pore in female opposite or anterior to median bulb, in male usually posterior to median bulb. No pre-adult vermiform female stage (except in *Meloinema*).

Mature female: Swollen, sedentary, round, oval to pear-shaped with a projecting neck. Cuticle moderately thick, striated, generally forming typical, fingerprint-like perineal pattern terminally. No cyst stage. Vulva subterminal or terminal. Anus located near vulval lip; tail rudimentary or absent. Stylet under 25 µm long in *Meloidogyne* (but 30–35 µm long in *Meloinema*). Median bulb oval or rounded, usually offset, with large refractive thickenings. Didelphic–prodelphic; ovaries coiled. Most eggs not retained in body but laid. Large rectal glands present, gelatinous matrix present.

Male: Vermiform, migratory, generally non-feeding, over 1 mm long, posterior end twisted through 90–180°, developing by metamorphosis within a saccate juvenile. Labial region rather low and continuous; amphidial apertures large transverse slits; labial cap large, prominent; framework moderately sclerotized, lateral sectors wider than submedian sectors. Stylet strong, usually over 20 µm long, basal knobs prominent. Tail short or absent, lacking a bursa (except *Bursadera*). Spicules large (25–64 µm), distally pointed. Gubernaculum linear to trough-shaped, not protrusible. Cloacal lips non-tuboid, generally with hypopygium.

Juveniles: Second stage migratory and infective. Third- and fourth-stage juveniles swollen, without stylet in type genus. In *Meloinema*, third- and fourth-stage juveniles vermiform. Labial region low, anteriorly flattened or rounded. Lateral sectors wider than submedian sectors, labial disc distinct in type genus. Stylet weak to moderately developed, less than 20 µm long in type genus but strongly developed in *Meloinema*. Tail elongate-conoid, with minutely rounded tip and conspicuous terminal hyaline portion. Phasmids dot-like, located on tail, usually anterior to middle.

Remarks: *Meloidogyninae* differs from *Heteroderinae* by its members inciting root-galls and having the lateral sectors of the labial framework wider than the submedian sectors, weaker labial sclerotization and stylet, excretory pore of mature female located opposite or anterior to median bulb, and third- and fourth-stage juveniles lacking a stylet in the type genus.

Type genus:

Meloidogyne Göldi, 1887

Other genera:

Meloinema Choi & Geraert, 1974

= *Nacobdodera* Golden & Jensen, 1974

Bursadera Ivanova & Krall, 1985

Genus *Meloidogyne* Göldi, 1887

= *Hypsoperine* Sledge & Golden, 1964

= *Hypsoperine* (*Hypsoperine*) Sledge & Golden, 1964 (Siddiqi, 1986)

= *Hypsoperine* (*Spartonema*) (Siddiqi, 1986)

= *Spartonema* Siddiqi, 1986

Diagnosis (modified after Siddiqi, 2000): *Meloidogyninae*. Root-gall inciting.

Mature female: Round to pear-shaped with short projecting neck, white, sedentary. No cyst stage. Vulva and anus located close together, terminal; perineum with a fingerprint-like cuticular pattern, usually flattened, rarely elevated. Phasmids dot-like, slightly anterior to, and on either side of, anus. Cuticle striated. Stylet slender, generally 12–15 µm long, with small basal knobs. Excretory pore anterior to median bulb, often just posterior to base of stylet. Genital tracts paired, prodelphic, convoluted. Six large rectal glands secreting gelatinous material in which eggs are deposited;³ eggs not retained in body.

Male: Vermiform, up to 2 mm long, tail end twisted, developing by metamorphosis within a swollen juvenile. Cuticle strongly annulated; lateral field with four incisures. Labial region not sharply offset, with distinct labial disc and few (1–3) annules; lateral sectors wider than submedian sectors, appearing as ‘cheeks’. Stylet robust (18–25 µm), with large basal knobs. Pharyngeal glands lying mostly ventral to intestine. Spicules slender, generally 25–33 µm long, gubernaculum 7–11 µm long. Testis single, but paired when sex reversal occurs. Tail rounded. Phasmids dot-like, located near cloacal aperture, which is subterminal. Bursa absent.

Juveniles: First stage with a blunt tail tip, moulting within egg; second and third moults occurring within cuticle of second stage. Second stage vermiform, migratory, infective, straight to arcuate habitus upon death. Labial region with coarse annules (1–4), a distinct labial disc, framework lightly sclerotized, lateral sectors wider than submedian sectors, stylet slender, under 20 µm, excretory pore posterior to hemizonid. Median bulb with large oval refractive thickenings. Tail with conspicuous hyaline region, tip narrow, irregular in outline. Third stage sedentary, swollen, sausage-shaped with a short blunt

³ Rectal glands not developed and no egg mass formed in *M. spartinae* and *M. kikuyensis*.

tail. Stylet absent. Fourth stage sedentary, swollen, with terminal anus. Stylet absent.

Note: The genus *Caconema* Cobb, 1924 has been regarded as a junior synonym of *Meloidogyne*, an action accepted by many taxonomists including Siddiqi (1986). However, after discussion with Andrassy (*in litt.*), Siddiqi (2000) pointed out that *Caconema* was based on *H. radicolica* Greeff as type, Müller's misattribution of his root-knot species to that described by Greeff finally coming home to roost. Greeff's species (*sensu* Greeff, not Müller) is also the type of *Subanguina* Paramonov, 1967 and, therefore, *Caconema* and *Subanguina* are, both being based on the same type species, objective synonyms. *Caconema* is, of course, the senior name, but Siddiqi (2000) argued the case that it should be regarded as an invalid senior synonym and sup-

pressed by the International Code of Zoological Nomenclature (ICZN) on the basis that it was a *nomen oblitum*, whereas *Subanguina* had been widely accepted and used as a valid taxon. Such a ruling has yet to be made by the ICZN.

3.4 List of Species and Synonyms

The following list is based on that of Siddiqi (2000) but includes those species that he regarded as belonging to the genus *Hypsoperine*. A full synonymy is provided together with bibliographic references for all taxonomic authorities. The Principle of Coordination (Article 43.1, International Code of Zoological Nomenclature, 1999) is followed for authorities.

Type species:

Meloidogyne exigua Göldi, 1887

= *Heterodera exigua* (Göldi, 1887) Marcinowski, 1909

Other species:

Meloidogyne acronea Coetzee, 1956

= *Hypsoperine acronea* (Coetzee, 1956) Sledge & Golden, 1964

= *Hypsoperine (Hypsoperine) acronea* (Coetzee, 1956) Sledge & Golden, 1964 (Siddiqi, 1986)

Meloidogyne actinidiae Li & Yu, 1991

Meloidogyne africana Whitehead, 1960

Meloidogyne aquatilis Ebsary & Eveleigh, 1983

Meloidogyne arabicida López & Salazar, 1989

Meloidogyne ardenensis Santos, 1968

= *Meloidogyne deconincki* Elmiligy, 1968

= *Meloidogyne litoralis* Elmiligy, 1968

Meloidogyne arenaria (Neal, 1889) Chitwood, 1949

= *Anguillula arenaria* Neal, 1889

= *Tylenchus arenarius* (Neal, 1889) Cobb, 1890

= *Heterodera arenaria* (Neal, 1889) Marcinowski, 1909

= *Meloidogyne arenaria arenaria* (Neal, 1889) Chitwood, 1949

= *Meloidogyne arenaria thamesi* Chitwood *in* Chitwood, Specht & Havis, 1952

= *Meloidogyne thamesi* Chitwood *in* Chitwood, Specht & Havis, 1952 (Goodey, 1963)

= *Meloidogyne thamesi gyulai* Amin, 1993

= *Meloidogyne gyulai* Amin, 1993

Meloidogyne artiellia Franklin, 1961

Meloidogyne baetica Castillo, Vovlas, Subbotin & Troccoli, 2003

Meloidogyne brasiliensis Charchar & Eisenback, 2002

Meloidogyne brevicauda Loos, 1953

Meloidogyne californiensis Abdel-Rahman & Maggenti, 1987

= *Meloidogyne californiensis* Abdel-Rahman, 1981 (= *nomen nudum*)

Meloidogyne camelliae Golden, 1979

Meloidogyne caraganae Shagalina, Ivanova & Krall, 1985

Meloidogyne carolinensis Eisenback, 1982

= *Meloidogyne carolinensis* Fox, 1967 (= *nomen nudum*)

Meloidogyne chitwoodi Golden, O'Bannon, Santo & Finley, 1980

- Meloidogyne chosenia* Eroshenko & Lebedeva, 1992
Meloidogyne christiei Golden & Kaplan, 1986
Meloidogyne cirricauda Zhang & Weng, 1991
Meloidogyne citri Zhang, Gao & Weng, 1990
Meloidogyne coffeicola Lordello & Zamith, 1960
 = *Meloidodera coffeicola* (Lordello & Zamith, 1960) Kirjanova, 1963
Meloidogyne cruciani García-Martínez, Taylor & Smart, 1982
Meloidogyne cynariensis Pham,⁴ 1990
Meloidogyne decalineata Whitehead, 1968
Meloidogyne donghaiensis Zheng, Lin & Zheng, 1990
Meloidogyne dunensis Paolomaes Rius, Vovlas, Troccoli, Liebanas, Landa & Castillo, 2007
Meloidogyne duytsi Karssen, van Aelst & van der Putten, 1998
Meloidogyne enterolobii Yang & Eisenback, 1983
 = *Meloidogyne mayaguensis* Rammah & Hirschmann, 1988
Meloidogyne ethiopica Whitehead, 1968
Meloidogyne fallax Karssen, 1996
Meloidogyne fanzhiensis Chen, Peng & Zheng, 1990
Meloidogyne floridensis Handoo, Nyczepir, Esmenjaud, van der Beck, Castagnone-Sereno, Carta, Skantar & Higgins, 2004
Meloidogyne fujianensis Pan, 1985
 = *Meloidogyne fujianensis* Pan, Ling & Wang, 1988 (= objective junior homonym)
Meloidogyne graminicola Golden & Birchfield, 1965
Meloidogyne graminis (Sledge & Golden, 1964) Whitehead, 1968
 = *Hypsoperine graminis* Sledge & Golden, 1964
 = *Hypsoperine (Hypsoperine) graminis* Sledge & Golden, 1964 (Siddiqi, 1986)
Meloidogyne hainanensis Liao & Feng, 1995
Meloidogyne hapla Chitwood, 1949
Meloidogyne haplanaria Eisenback, Bernard, Starr, Lee & Tomaszewski, 2004
Meloidogyne hispanica Hirschmann, 1986
Meloidogyne ichinohei Araki, 1992
Meloidogyne incognita (Kofoid & White, 1919) Chitwood, 1949
 = *Oxyuris incognita* Kofoid & White, 1919
 = *Heterodera incognita* (Kofoid & White, 1919) Sandground, 1923
 = *Meloidogyne incognita incognita* (Kofoid & White, 1919) Chitwood, 1949
 = *Meloidogyne acrita* Chitwood, 1949
 = *Meloidogyne incognita acrita* Chitwood, 1949
 = *Meloidogyne kirjanovae* Terenteva, 1965
 = *Meloidogyne elegans* da Ponte, 1977
 = *Meloidogyne incognita grahami* Golden & Slana, 1978
 = *Meloidogyne grahami* Golden & Slana, 1978
 = *Meloidogyne incognita wartellei* Golden & Birchfield, 1978
 = *Meloidogyne wartellei* Golden & Birchfield, 1978
Meloidogyne indica Whitehead, 1968
Meloidogyne inornata Lordello, 1956a
 = *Meloidogyne incognita inornata* Lordello, 1956a
Meloidogyne izalcoensis Carneiro, Almeida, Gomes & Hernández, 2005
Meloidogyne javanica (Treub, 1885) Chitwood, 1949
 = *Heterodera javanica* Treub, 1885
 = *Tylenchus (Heterodera) javanicus* (Treub, 1885) Cobb, 1890
 = *Anguillula javanica* (Treub, 1885) Laverigne, 1901a

⁴ Cited as 'Pham Thanh Binh' after the species name in the original paper.

- = *Meloidogyne javanica javanica* (Treub, 1885) Chitwood, 1949
 = *Meloidogyne javanica bauruensis* Lordello, 1956b
 = *Meloidogyne bauruensis* Lordello, 1956b
 = *Meloidogyne lordelloi* da Ponte, 1969
 = *Meloidogyne lucknowica* Singh, 1969
Meloidogyne jianyangensis Yang, Hu, Chen & Zhu, 1990
 = *Meloidogyne jianyangensis* Zhu, Lan, Hu, Yang & Wang, 1991⁵ (= objective junior homonym)
Meloidogyne jinanensis Zhang & Su, 1986
Meloidogyne kikuyensis De Grisse, 1961
 = *Spartonema kikuyense* (De Grisse, 1961) Siddiqi, 2000
Meloidogyne konaensis Eisenback, Bernard & Schmitt, 1995
Meloidogyne kongi Yang, Wang & Feng, 1988
Meloidogyne kralli Jepson, 1984
Meloidogyne lini Yang, Hu & Xu, 1988
Meloidogyne lusitanica Abrantes & Santos, 1991
Meloidogyne mali Itoh, Ohshima & Ichinohe, 1969
Meloidogyne maritima Jepson, 1987
Meloidogyne marylandi Jepson & Golden *in* Jepson, 1987
Meloidogyne megadora Whitehead, 1968
Meloidogyne megalatyla Baldwin & Sasser, 1979
Meloidogyne mersa Siddiqi & Booth, 1991
 = *Meloidogyne (Hypsoperine) mersa* Siddiqi & Booth, 1991
Meloidogyne microcephalus Cliff & Hirschmann, 1984
Meloidogyne microtyla Mulvey, Townshend & Potter, 1975
Meloidogyne mingnanica Zhang, 1993
Meloidogyne minor Karssen, Bolk, van Aelst, van den Beld, Kox, Korthals, Molendijk, Zijlstra, van Hoof & Cook, 2004
Meloidogyne morocciensis Rammah & Hirschmann, 1990
Meloidogyne naasi Franklin, 1965a
Meloidogyne nataliae Golden, Rose & Bird, 1981
Meloidogyne oryzae Maas, Sanders & Dede, 1978
*Meloidogyne oteifae*⁶ Elmiligy, 1968
Meloidogyne ottersoni (Thorne, 1969) Franklin, 1971
 = *Hypsoperine ottersoni* Thorne, 1969
 = *Hypsoperine (Hypsoperine) ottersoni* Thorne, 1969 (Siddiqi, 1986)
Meloidogyne ovalis Riffle, 1963
Meloidogyne panyuensis Liao, Yang, Feng & Karssen, 2005
 = *Meloidogyne panyuensis* Liao, 2001 (= *nomen nudum*)
Meloidogyne paranaensis Carneiro, Carneiro, Abrantes, Santos & Almeida, 1996
Meloidogyne partityla Kleynhans, 1986b
Meloidogyne petuniae Charchar, Eisenback & Hirschmann, 1999
Meloidogyne phaseoli Charchar, Eisenback, Charchar & Boiteau, 2008b
Meloidogyne pini Eisenback, Yang & Hartman, 1985
Meloidogyne piperi Sahoo, Ganguly & Eapen, 2000
Meloidogyne pisi Charchar, Eisenback, Charchar & Boiteau, 2008a
Meloidogyne platani Hirschmann, 1982
Meloidogyne propora Spaul, 1977
 = *Hypsoperine propora* (Spaul, 1977) Siddiqi, 1986

⁵ The authors cite this name as a new species, thereby creating, albeit unintentionally, a junior objective homonym.

⁶ Original spelling *oteifae*.

- = *Hypsoperine (Hypsoperine) propora* (Spaull, 1977) Siddiqi, 1986
Meloidogyne querciana Golden, 1979
Meloidogyne salasi López, 1984
Meloidogyne sasseri Handoo, Huettel & Golden, 1994
Meloidogyne sewelli Mulvey & Anderson, 1980
Meloidogyne silvestris Castillo, Vovlas, Troccoli, Liébanas, Palomares Rivs & Landa, 2009
Meloidogyne sinensis Zhang, 1983
Meloidogyne spartinae (Rau & Fassuliotis, 1965) Whitehead, 1968
= *Hypsoperine spartinae* Rau & Fassuliotis, 1965
= *Hypsoperine (Spartonema) spartinae* Rau & Fassuliotis, 1965 (Siddiqi, 1986)
= *Spartonema spartinae* (Rau & Fassuliotis, 1965) Siddiqi, 1986
Meloidogyne subarctica Bernard, 1981
Meloidogyne suginamiensis Toida & Yaegashi, 1984
Meloidogyne tadshikistanica Kirjanova & Ivanova, 1965
Meloidogyne thailandica Handoo, Skantar, Carta & Erbe, 2005
Meloidogyne trifoliophila Bernard & Eisenback, 1997
Meloidogyne tritricoryzae Gaur, Saha & Khan, 1993
Meloidogyne turkestanica Shagalina, Ivanova & Krall, 1985
Meloidogyne ulmi Marinari-Palmisano & Ambrogioni, 2000
Meloidogyne vandervegtei Kleynhans, 1988

Species inquirendae:

- Meloidogyne marioni* (Cornu, 1879) Chitwood & Oteifa, 1952
= *Anguillula marioni* Cornu, 1879
= *Heterodera marioni* (Cornu, 1879) Marcinowski, 1909
Meloidogyne megriensis (Poghossian, 1971) Esser, Perry & Taylor, 1976
= *Hypsoperine megriensis* Poghossian, 1971
= *Hypsoperine (Hypsoperine) megriensis* Poghossian, 1971 (Siddiqi, 1986)
Meloidogyne poghossianae Kirjanova, 1963
= *Meloidogyne acronea apud* Poghossian, 1961 *nec M. acronea* Coetzee, 1956
Meloidogyne vialae (Lavergne, 1901b) Chitwood & Oteifa, 1952
= *Anguillula vialae* Lavergne, 1901b
= *Heterodera vialae* (Lavergne, 1901b) Marcinowski, 1909

Nomina nuda:

- Meloidogyne californiensis* Abdel-Rahman, 1981
Meloidogyne carolinensis Fox, 1967
Meloidogyne goeldii Santos, 1997
Meloidogyne panyuensis Liao, 2001 *nec M. panyuensis* Liao *et al.*, 2005
Meloidogyne zhanjiangensis Liao, 2001

Notes

1. Siddiqi (1986, 2000) cited '*Meloidogyne goeldi* Lordello, 1951' as being proposed as a *nomen novum* for *M. marioni*. This was repeated by Karssen and Moens (2006) in their species list, albeit under the genus *Heterodera*, but is incorrect, apparently stemming from Lordello's citation of the genus and authority being misinterpreted as a binomen (see Lordello, 1951, English Summary, p. 250).
2. In the Chinese literature a species name may be cited as 'n. sp.' subsequent to the original proposal – and with different authors (e.g. *M. fujianensis* and *M. jianyangensis*). Each such subsequent citation appears to be a junior objective homonym and is probably also a *nomen nudum*.
3. The Index of Organism Names (see <http://www.organismnames.com/>, accessed 3 April 2008) lists the combination '*Meloidogyne zhanjiangensis*'. The publication authority and date for this name are not cited therein, the binomen presumably being culled from other published sources. There is, however, a web reference to a Chinese PhD thesis entitled 'Study on the identification and polymorphism of

root-knot nematodes (*Meloidogyne*)' by J.L. Liao, where the combination '*Meloidogyne zhanjiangensis* n. sp.' occurs; '*Meloidogyne panyuensis* n. sp.' is also mentioned, although this species was subsequently formally described by Liao *et al.* (2005). There is also a web reference to a paper entitled 'Description of *Meloidogyne zhanjiangensis* n. sp. from China' by Liao and Feng. This was supposedly published in the *Russian Journal of Nematology*, volume 11(2) in 2003 (www.nsf.gov.cn/nsfc/cen/00/kxb/sm/wuchu04.doc, accessed 3 April 2008). However, the only paper by these authors in that issue of the journal is an abstract of a description of a new species of *Meloidogyne* from pea in Guangdong province, China (see Liao and Feng, 2003). No mention is made of a specific name in either the title or text in this abstract (although it seems to be the same article as mentioned above), reference to the specific epithet probably being removed by the editor to avoid creating a *nomen nudum*.

According to Chen Mian-Cai of South China Agricultural University (C. Mian-Cai, China, April 2008, personal communication), the species name was originally proposed in a PhD thesis submitted by J.L. Liao to the university in 2001 (Liao, 2001), although to date a description has not been published in a journal. The binomen was cited by Rui *et al.* (2005), along with a brief set of measurements, pictures of the perineal pattern, J2 and female anterior region, together with Est and Mdh isozyme profiles, but with no formal proposal/description. At the present time, the status of this name is unclear and it is prudent to regard it as a *nomen nudum*.

3.5 Identification

Accurate identification of root-knot nematodes is crucial for effective disease control and depends on rapid and accurate classification of the pathogens involved so that appropriate control measures may be taken. In addition, sound decisions regarding quarantine of imported and exported plant material and commodities also demand timely and accurate diagnostics. None the less, the identification of root-knot nematodes to species level is fraught with difficulty. Conserved morphology, variable morphometrics, host effects, intraspecific variation, the parthenogenetic mode of reproduction, existence of cryptic species or species swarms, and the ever-increasing number of described species – the diagnosis and relationships of many of which vary from less than ideal to dubious – all serve to obfuscate the clear interspecific boundaries that we yearn for. To add to the confusion, there is the not-inconsiderable problem of 'species concept' in organisms that predominantly rely on a parthenogenetic reproductive strategy.

Verification of mixed populations and/or detection of rare species requires identification techniques other than the North Carolina differential host test (see section 3.5.7 below), including morphological (perineal pattern of adult females; male, female and J2 labial region shape, and stylet morphology; length and shape of J2 tail) and, in some cases, biochemical or molecular methodologies. Detailed diagnostic characters differentiating *Meloidogyne* species have been given by authors such as Eisenback *et al.* (1981), Eisenback (1985),

Hirschmann (1985), Jepson (1987), Taylor (1987) and Eisenback and Triantaphyllou (1991). They are also covered in Eisenback and Hunt, Chapter 2, this volume.

For many years the form of the perineal pattern of the mature female and various morphometric and morphological features of the J2 were relied upon in species determination. To these were added features of the (often only rarely produced) male, such as the form of the labial region, including the annulation, and form of the stylet and basal knobs. With the increasing number of described species, however, the value of many of these characters, themselves showing often large intraspecific variation, was eroded almost to the point where robust identification tended to involve a fair measure of serendipity.

As an example, what may be termed the *incognita*-type of perineal pattern is now known to occur in a substantial number of species, some of which were commonly misidentified as *M. incognita* (see the work on South and Central American coffee nematodes by Carneiro *et al.*, 2004b, 2005). Isozyme electrophoresis has discriminated a number of these otherwise cryptic species but it is PCR-based molecular methodologies that currently carry the torch and our hopes for the future.

3.5.1 General techniques

For morphological observation, J2 and males can be recovered from fresh infected roots or egg masses incubated in Petri dishes with a small

amount of water. They may also be recovered from soil by sieving and Baermann funnel techniques. Females are dissected from infected roots after fixation overnight in 3% formaldehyde. Procedures for measuring and preparing specimens are as given in Golden and Birchfield (1972), except that some females have the anterior and posterior ends cut with a sharp knife, cleaned with a dental root canal file, and mounted permanently on a glass slide in a drop of lactophenol solution. Photomicrographs of perineal patterns, J2s and males can be done with a 35 mm or digital camera attached to a dissecting microscope.

For more details on killing, fixing, processing nematodes to glycerine, preparing temporary and permanent slide mounts, and preserving nematode structures in a life-like manner, the reader is referred to Whitehead (1968), Hooper (1970, 1986, 1990), Golden (1990) and Carta (1991).

3.5.2 Perineal pattern

The character most frequently used for *Meloidogyne* species identification is the morphology of the perineal pattern, which is located in the posterior body region of adult females. This area comprises the vulva–anus area (perineum), tail terminus, phasmids, lateral lines and surrounding cuticular striae. Preparation of perineal patterns (Fig. 3.6) for observation and identification has been covered by Taylor *et al.* (1955), Eisenback (1985), Franklin (1965b), Sasser and Carter (1982), Hartman and Sasser (1985), Hirschmann (1985), Jepson (1987), Riggs (1990) and Charchar and Eisenback (2000). A more detailed account on root-knot perineal pattern development was given by Karssen (2002). Figure 3.7 summarizes the form of perineal pattern in the 12 species of *Meloidogyne* that are considered in greater detail in this chapter.

3.5.3 Root staining

Many methods have been developed for staining and clearing nematode-infected root tissues. Staining with acid fuchsin-lactophenol or lactoglycerol are the most widely used methods. In addition, a method that utilizes chlorine bleach as a prestaining treatment has proven to be very reliable and is relatively simple to use (Byrd *et al.*, 1983). For more detail, see McBeth *et al.* (1941), Hooper (1986, 1990) and Hussey (1990).

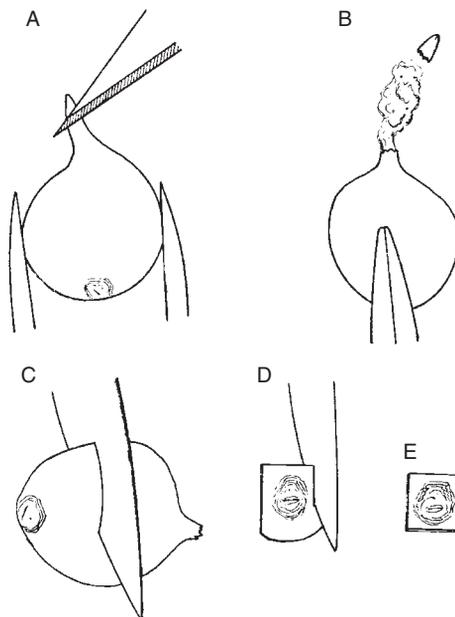


Fig. 3.6. How to cut perineal patterns. A, B: excised female with neck region removed and body contents gently expelled; C: posterior body with perineal pattern removed; D: trimming surplus cuticle around perineal pattern; E: trimmed perineal pattern ready for mounting. After Hartman and Sasser (1985).

3.5.4 Scanning electron microscopy

For scanning electron microscopy, living specimens are fixed in 3% glutaraldehyde solution buffered with 0.05 M phosphate (pH 6.8), dehydrated in a graded series of ethanol, critical-point dried from liquid CO₂ and sputter-coated with a 20–30 nm layer of gold–palladium. For more detail, the papers by Eisenback (1991) and Charchar and Eisenback (2000) are recommended; see also Eisenback and Hunt, Chapter 2, this volume.

3.5.5 Diagnostic characters

The most important diagnostic features used for identification of *Meloidogyne* spp. include: **Female.** Shape of body, labial region, stylet length, shape of stylet cone, shaft and basal knobs, nature of perineal pattern, including form of dorsal arch, lateral field, striae and tail terminus (see Fig. 3.7), and excretory pore/stylet length ratios (EP/ST). **Male.** Size, height and shape of labial cap, the number of annulations, diameter of the labial region as

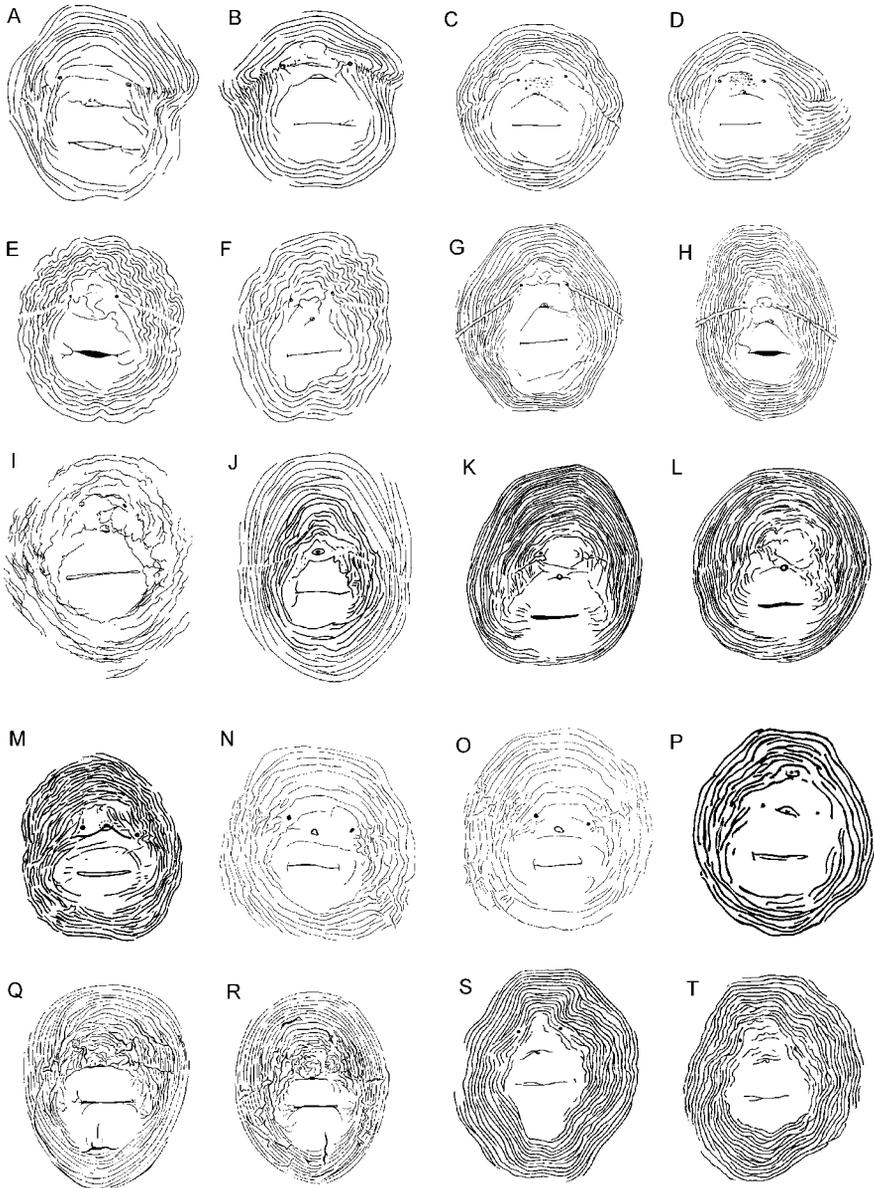


Fig. 3.7. Comparison of perineal patterns for 12 major species of *Meloidogyne*. A, B: *M. arenaria*; C, D: *M. hapla*; E, F: *M. incognita*; G, H: *M. javanica*; I: *M. acrona*; J: *M. chitwoodi*; K, L: *M. enterolobii*; M: *M. ethiopica*; N, O: *M. exigua*; P: *M. fallax*; Q, R: *M. graminicola*; S, T: *M. paranaensis*. Drawings not to scale. A–H, after Orton Williams (1972, 1973, 1974, 1975); I, after Page (1985); J, after Jepson (1985); K, L, after Rammah and Hirschmann (1988); M, after Whitehead (1968); N, O, courtesy of Janet Machon; P, after Karssen (1996); Q, R, after Mulk (1976); S, T, after Carneiro *et al.* (1996).

compared with the first body annule, stylet length, form of stylet cone, shaft and basal knobs, distance of the dorsal gland orifice (DGO) from the stylet base and length and form of spicule. **J2.** Body and

stylet length, form of labial region and shape of stylet knobs, location of the hemizonid in relation to the excretory pore, distance of DGO from stylet base, number of lines in the lateral field and shape

and length of the tail and hyaline terminus. For more details about these and other differentiating characters, see Whitehead (1968), Esser *et al.* (1976), Eisenback *et al.* (1981), Hirschmann (1985), Kleynhans (1986a), Jepson (1987), Eisenback and Triantaphyllou (1991), Karssen (2002) and Eisenback and Hunt, Chapter 2, this volume.

3.5.6 Root-knot or cyst-forming nematode?

Differentiating root-knot nematodes from cyst-forming nematodes is usually an easy task, regardless of developmental stage. However, in the interest of completeness these differences are summarized and compared in Table 3.1 and Fig. 3.8.

3.5.7 Differential host test

Variations in host range are known to occur in some species of root-knot nematodes, and attempts have been made to characterize these on the basis of differential host range. Sasser (1954) proposed a

simple method, based on responses to a series of differential hosts and the amount of galling induced, to identify four of the five species of *Meloidogyne* recognized by Chitwood (1949). Subsequently, this test was often a component in descriptions of new species, purporting to demonstrate a 'unique' host reaction (see also Sasser, 1979). This test became known as the 'North Carolina differential host test' and has been used to detect host races within the 'Chitwood species' (Sasser and Carter, 1982). The 'International *Meloidogyne* project' (IMP) summarized the responses of about 1000 populations of the four most common species of *Meloidogyne* and their races to differential hosts, and more details were provided by Taylor and Sasser (1978), Eisenback *et al.* (1981), Sasser and Carter (1982) and Hartman and Sasser (1985). As discussed by Moens *et al.* (Chapter 1, this volume), the differential host range test is currently out of favour as a diagnostic tool and has several drawbacks.

3.5.8 Gall form

Species of *Meloidogyne* typically cause galls on plant roots and other below-ground organs. However,

Table 3.1. Comparison between root-knot and cyst-forming nematodes.

Stage	Character	Root-knot	Cyst-forming
Second-stage infective juveniles	Body form	Slender, anterior body tapering	Robust, anterior body more parallel
	Labial region	Weakly cuticularized, not offset	Strongly cuticularized, offset
	Stylet Hyaline region	Slender, < 19 µm long Short, starting near tail tip	Robust, 20–30 µm long Long, well developed
Sedentary juveniles	Tail spike	Present	Absent
Male	Labial region	Weakly cuticularized, 2 annules	Strongly cuticularized, 4–5 annules
	Stylet	Slender	Robust
Mature female	Excretory pore	Anterior to median bulb valve plates	Posterior to median bulb valve plates
	Cuticle	Thin, white, not tanning to brownish colour on death	Thick, tanning to brownish colour on death
	Eggs	Deposited in external gelatinous egg mass, few retained in body	Mostly retained within body, occasionally a few laid into small egg sac
Biology	Host symptoms	Root galls almost always formed	No root galls formed
	Parasitic habit	Mature female usually endoparasitic	Mature female semi-endoparasitic
	Trophic system	Giant cells	Syncytia

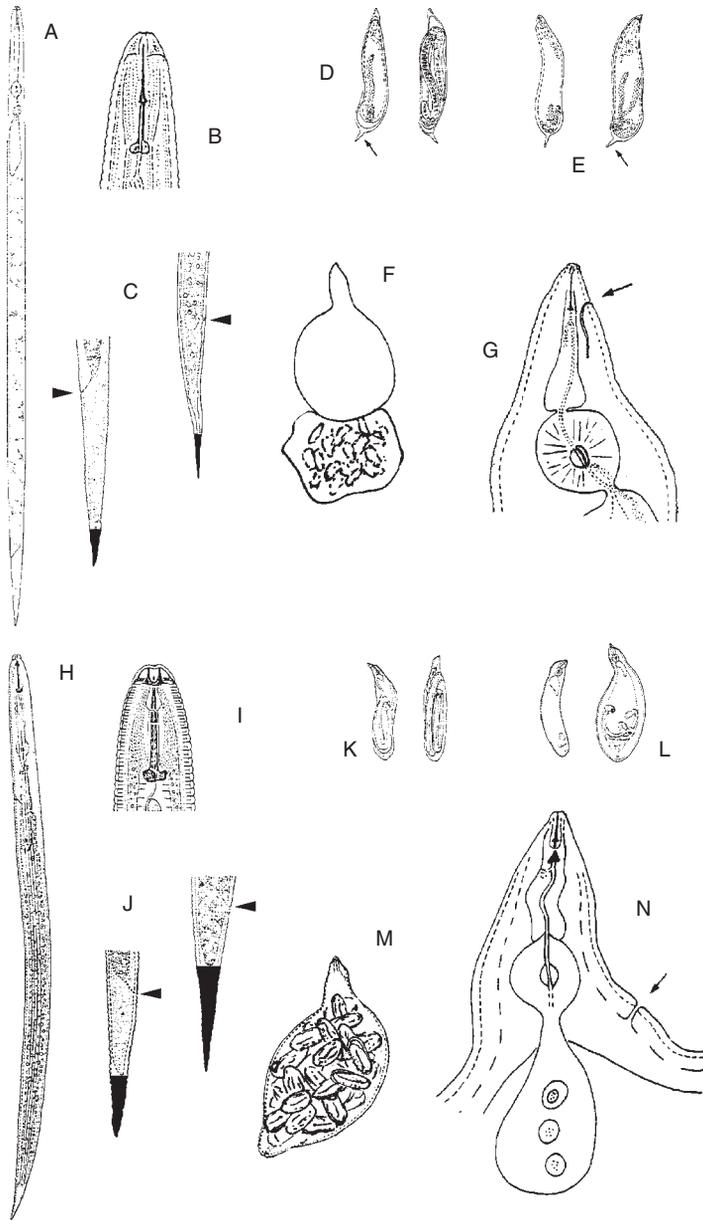


Fig. 3.8. Comparative morphology between root-knot and cyst-forming nematodes. A–G: root-knot nematode. H–N: cyst-forming nematode. A, H: infective J2; Note that the root-knot J2 is more slender. B, I: anterior region of J2, showing weaker labial sclerotization and spear development in B compared with I. C, J: tail region of J2, showing difference in hyaline region (indicated by black infill) as proportion of tail length (arrowhead points at anus in each case). D, K: development of male parasitic stages; Note presence of tail spike in D (arrow). E, L: development of female parasitic stages; Note presence of tail spike in E (arrow). F, M: mature female, showing eggs mostly laid into external gelatinous mass (F) or retained in body (M). G, N: anterior region of female, showing relative position of excretory pore (arrow), which is either anterior (G) or posterior (N) to the median bulb valve plates. Drawings not to scale and adapted from various sources.

they may also parasitize stems, leaves or flowers and incite galls in these tissues in several genera of plants (Lehman, 1985). *Meloidogyne* spp. are the most common and best-known nematodes that cause extensive root galls or 'root-knots', although a few species do not produce galls at all, e.g. *M. sasseri* (Handoo *et al.*, 1994).

The physical appearance and position of galls on roots can be of some assistance in diagnostics. For example, *M. javanica* and *M. incognita* tend to form large and irregular galls some distance from the root tip, whereas *M. exigua* galls on coffee are small, more or less spherical and located at the root tip. Galls of *M. graminicola* on rice are elongate and usually located just behind the root tip, affected roots assuming a characteristic hook-shape, while the relatively small and irregular galls of *M. hapla* often sport several lateral roots.

3.5.9 Isozyme phenotyping

Isozyme electrophoretic profiles, often using esterase and malate dehydrogenase, have been established for a number of species and can provide a useful, routine diagnostic test, particularly for morphologically variable species like *M. incognita* and *M. javanica* (see Esbenshade and Triantaphyllou, 1985a,b, 1987; Karssen *et al.*, 1995; Carneiro and Almeida, 2001; Carneiro *et al.*, 1998, 2000; Hernández *et al.*, 2004; Blok and Powers, Chapter 4, this volume). Some species, such as *M. arenaria*, show several different profiles, although this may be an indication of the existence of cryptic species. Although isozyme electrophoresis is perhaps the current diagnostic method of choice, with profiles accompanying the description of many new species, for example, it seems likely that PCR-based methodologies will soon usurp this method for many applications where finer resolution, particularly of intraspecific variation, is paramount.

3.5.10 Molecular diagnostics

There is no denying that PCR-based methodologies are of ever-increasing importance in species diagnostics and phylogeny within the genus *Meloidogyne*. Techniques include RFLP (restriction fragment length polymorphism) profiles of the ITS (internal transcribed spacer) region of rDNA, RAPD (random amplified polymorphic DNA)

fragments, 18S rDNA sequences, satellite DNA probes and species-specific primers. Recent papers include De Ley *et al.* (2002) and Tigano *et al.* (2005), both using sequences of the 18S rDNA to construct phylogenies, while the latter also employed IGS (intergenic spacer) mitochondrial rDNA sequences. Carta *et al.* (2006) recommended molecular protocols for identification of root-knot nematodes on potato. Molecular approaches are covered in greater detail in Blok and Powers, Chapter 4 and Adams *et al.*, Chapter 5, this volume.

3.6 Principal Species

The following 12 species have been selected for further discussion either because they are common, economically important and of worldwide distribution (e.g. *M. arenaria*, *M. hapla*, *M. incognita*, *M. javanica*), or because they represent more regionally constrained species that may be damaging to specific major crops (e.g. *M. chitwoodi*, *M. ethiopica*, *M. fallax*, *M. graminicola*) or have potential as emergent pests. To facilitate comparisons, the four commonest species are presented first, the remainder following in alphabetical order. Each species is illustrated (Figs 3.9–3.20) and perineal patterns are juxtaposed in Fig. 3.7. The data presented here were obtained from various sources, including Jepson (1987), Karssen and Moens (2006), and original descriptions and/or redescrptions.

3.6.1 *Meloidogyne arenaria* (Fig. 3.9)

Morphology: **Female.** Pear-shaped, no posterior terminal protuberance. Stylet 13–17 µm long, cone curved dorsally, gradually tapering to blunt tip anteriorly; shaft broad, cylindrical, gradually widening posteriorly; basal knobs rounded to teardrop-shaped, offset. Perineal pattern variable, rounded to ovoid with fine to coarse striae. Dorsal arch low, flattened with striae smooth or slightly wavy, continuous or broken, slightly bent towards tail tip at lateral line; generally forming shoulders on lateral portion of arch. Dorsal and ventral striae often meeting at an angle at lateral lines; lateral field distinct, slightly irregular. **Male.** Labial region not offset, smooth, rarely with one or two incomplete annulations, labial disc more or less rounded, slightly raised above level of medial lips, lateral lips usually absent (remnants

occasionally present). Stylet 20–28 μm long, basal knobs offset, angular or more amalgamated, DGO = 4–8 μm . **J2.** L (body length) = 392–605 μm , hemizonid one to three annules anterior to excretory pore, tail = 44–69 μm with rounded to pointed tail tip and indistinct 6–13 μm long hyaline region.

Hosts: Extremely polyphagous, attacking both monocotyledons and dicotyledons.

Distribution: Worldwide; found in most of the warmer regions of the world and frequently encountered in glasshouses in cooler climates.

Isozymes: Populations of *M. arenaria* are variable in isozyme phenotype (Esbenshade and Triantaphyllou, 1985a,b). Three phenotypes of esterase activity commonly occur – namely, A1, A2, and A3 – and several other phenotypes occur less commonly. The phenotypes A1 and A2

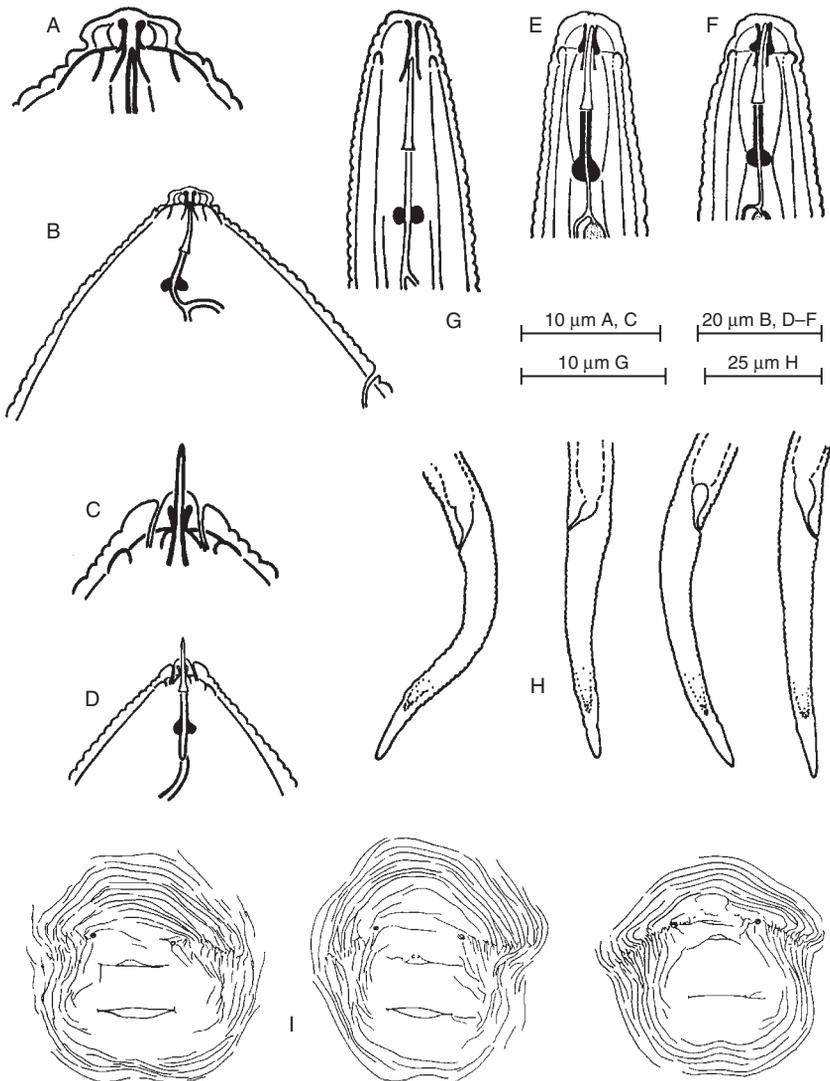


Fig. 3.9. *Meloidogyne arenaria*. A–D: female anterior region; E, F: male anterior region; G: J2 anterior region; H: J2 tail regions; I: perineal patterns. A–H, after Whitehead (1968), courtesy of *Transactions of the Zoological Society of London*; I, after Orton Williams (1975), courtesy of CAB International.

include several cytological forms of *M. arenaria*, whereas phenotype A3 includes only the most typical cytological form with a somatic chromosome number of 51–56. Some populations of *M. arenaria* have atypical esterase phenotypes: namely, S1-M1, S2-M1 and M3-F1. The malate dehydrogenase phenotype is either N1 or N3, according to population.

Remarks: One of the four commonest species worldwide. Typically inciting large, irregular galls. Part of a confusing species complex.

3.6.2 *Meloidogyne hapla* (Fig. 3.10)

Morphology: **Female.** Pear-shaped, terminal protuberance absent. Stylet 13–17 μm long, basal knobs small, rounded, offset. Perineal pattern rounded, low dorsal arch, characteristic punctations usually present near anus, fine striae, lateral field present. **Male.** Labial region offset, labial disc not usually elevated, lateral lips present. Stylet 19–22 μm long, basal knobs small, rounded, offset. DGO = 4–5 μm . **J2.** L = 360–500 μm , hemizonid anterior to excretory pore, tail = 48–70 μm , hyaline region often irregular in form, tail tip finely rounded.

Hosts: Mainly dicotyledonous plants.

Distribution: Common in temperate areas and at higher altitudes in the tropics.

Isozymes: Most populations show the H1 esterase phenotype (Esbensshade and Triantaphyllou, 1985a,b). One population from France does not have any major esterase activity, and another population from Minnesota, USA, has an A1 esterase phenotype identical to *M. arenaria*. The malate dehydrogenase H1 phenotype is unique for this species.

Remarks: One of the four commonest species worldwide. Galls are usually relatively small and may bear subsidiary roots.

3.6.3 *Meloidogyne incognita* (Fig. 3.11)

Morphology: **Female.** Pear-shaped, no posterior terminal protuberance. Stylet 15–16 μm long, basal knobs rounded, offset. Perineal pattern oval to rounded, typically with high, squared, dorsal arch, striae usually wavy, lateral field absent or weakly demarcated by forked striae. **Male.** Labial region not offset, labial disc elevated, lateral lips usually

absent. Stylet 23–26 μm long, basal knobs offset, rounded to transversely elongate. DGO = 2–4 μm . **J2.** L = 350–450 μm , hemizonid anterior or adjacent to excretory pore, tail = 43–65 μm with 6–14 μm long hyaline region, rounded tail tip.

Hosts: Extremely polyphagous, attacking both monocotyledons and dicotyledons.

Distribution: Worldwide; restricted to protected cultivation in temperate regions.

Isozymes: The unique esterase II type and the malate dehydrogenase N1 type were described by Esbensshade and Triantaphyllou (1985a,b). Variability of esterase activity is small, only one population not having the typical phenotype. The malate dehydrogenase phenotype N1 is similar to that of *M. javanica*, *M. exigua* and some populations of *M. arenaria*.

Remarks: One of the four commonest species worldwide. Typically inciting large, usually irregular, galls. Member of a confusing species complex.

3.6.4 *Meloidogyne javanica* (Fig. 3.12)

Morphology: **Female.** Pear-shaped, no posterior terminal protuberance. Stylet 14–18 μm long, basal knobs ovoid, offset. Perineal pattern rounded, low dorsal arch; striae smooth, tail whorl often distinct, lateral field distinct, clearly demarcated from striae by more or less parallel lines. **Male.** Labial region not offset, labial disc not elevated, lateral lips absent. Stylet 19–24 μm long, basal knobs ovoid, offset. DGO = 3–5.5 μm . **J2.** L = 400–560 μm , hemizonid anterior or adjacent to excretory pore, tail = 47–60 μm with 9–18 μm long hyaline region, finely rounded tail tip.

Hosts: Extremely polyphagous, attacking both monocotyledons and dicotyledons.

Distribution: Worldwide; restricted to protected cultivation in temperate regions.

Isozymes: The esterase phenotype is J3, J2 or J2a (Esbensshade and Triantaphyllou, 1985a,b; Tomaszewski *et al.*, 1994; Castro *et al.*, 2003) and the malate dehydrogenase is of the N1 type (Esbensshade and Triantaphyllou, 1985a,b). Most populations of *M. javanica* have a malate dehydrogenase phenotype N1, similar to that of *M. incognita*, *M. exigua* and some populations of *M. arenaria*. One population of *M. javanica* from Bangladesh and one from Korea have the N3 phenotype, similar to that of some populations of *M. arenaria*.

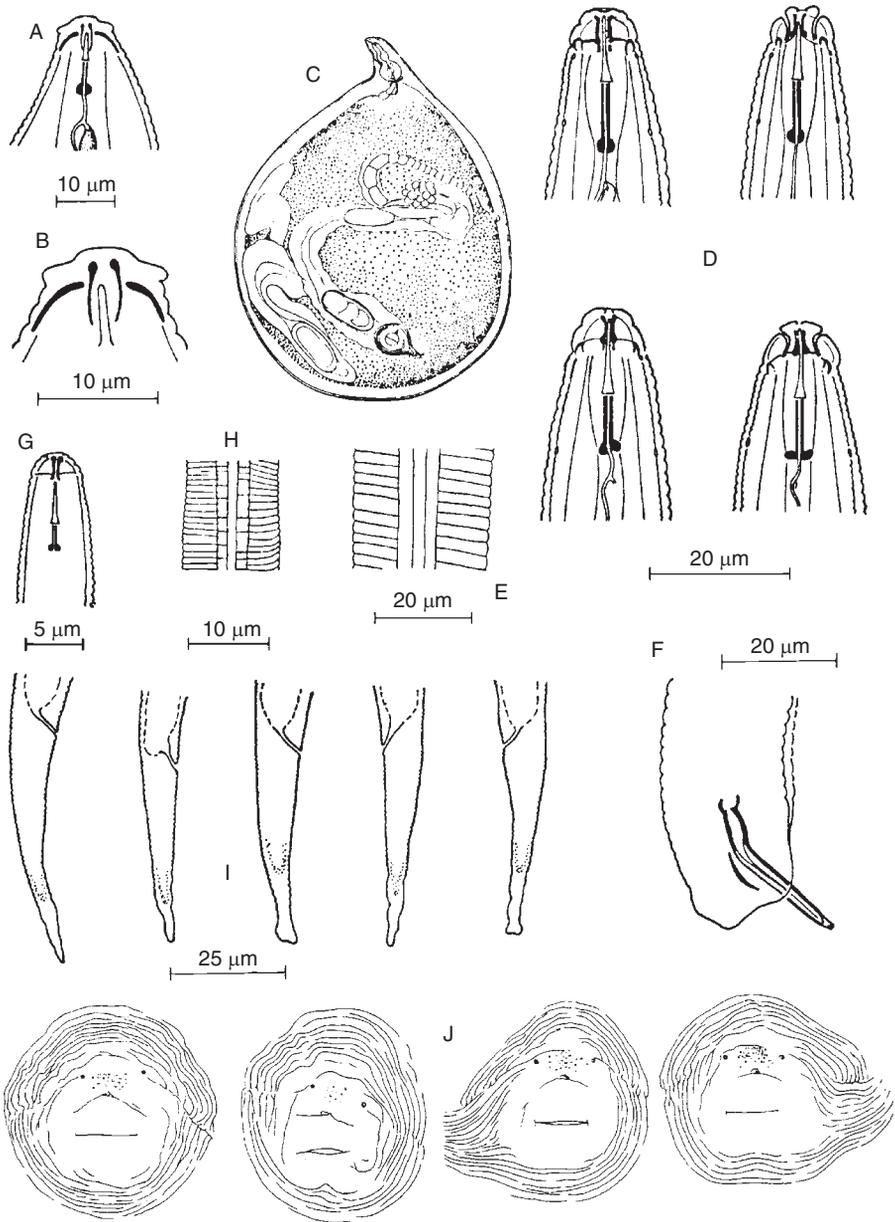


Fig. 3.10. *Meloidogyne hapla*. A, B: female anterior region; C: entire female; D: male anterior region; E: male lateral field; F: male tail; G: J2 anterior region; H: J2 lateral field at mid-body; I: J2 tail regions; J: perineal patterns. A–I, after Whitehead (1968), courtesy of *Transactions of the Zoological Society of London*; J, after Orton Williams (1974), courtesy of CAB International.

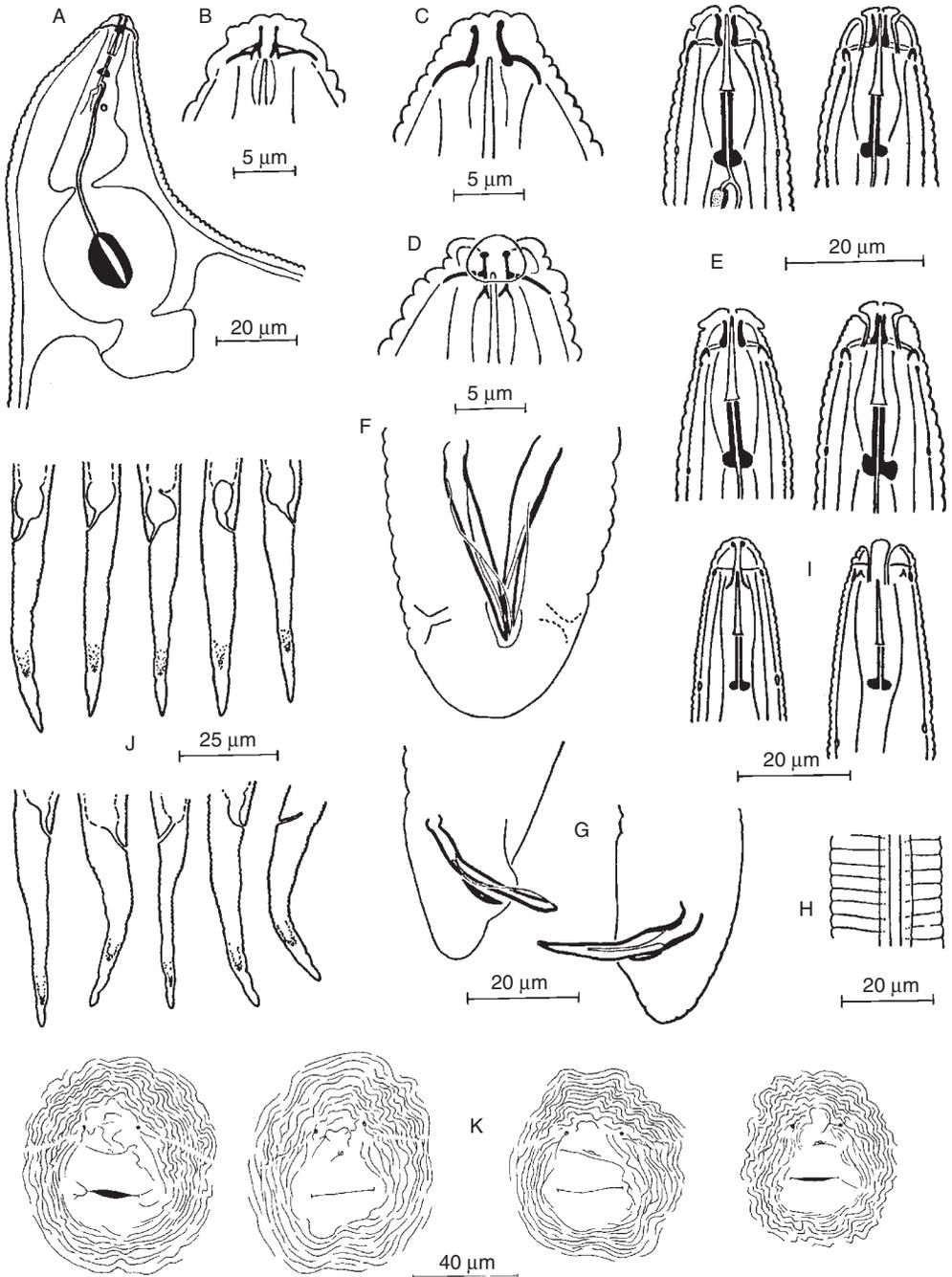


Fig. 3.11. *Meloidogyne incognita*. A: female pharyngeal region; B–D: female anterior region; E: male anterior region; F–G: male tail region; H: male lateral field; I: J2 anterior region; J: J2 tail regions; K: perineal patterns. A–J, after Whitehead (1968), courtesy of *Transactions of the Zoological Society of London*; K, after Orton Williams (1973), courtesy of CAB International.

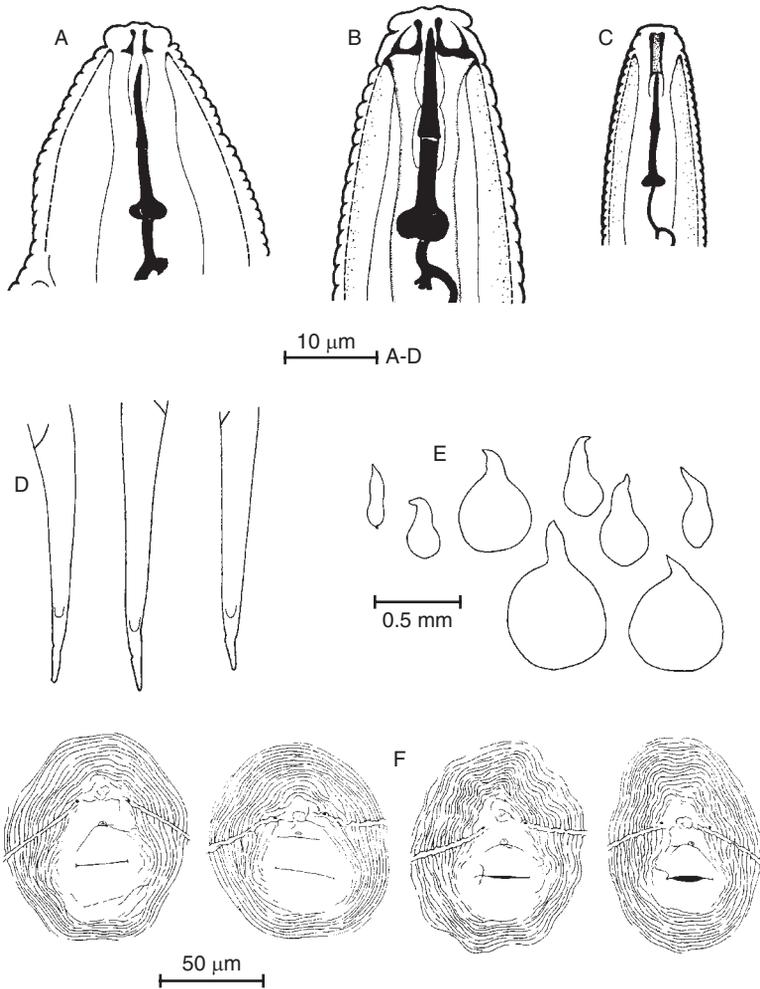


Fig. 3.12. *Meloidogyne javanica*. A: female pharyngeal region, lateral view; B: male anterior region; C: J2 anterior region; D: J2 tail regions; E: entire females; F: perineal pattern variation. A–D after Jepson (1987) and E, F after Orton Williams (1972), courtesy of CAB International.

Remarks: One of the four commonest species worldwide. Typically inciting large, irregular galls.

3.6.5 *Meloidogyne acronea* (Fig. 3.13)

Morphology: **Female.** Oval to spherical, perineal region situated on terminal protuberance. Stylet 10–14 µm long, basal knobs rounded, offset. Perineal pattern rounded, dorsal arch low, striae faint, intermittent, often broken on one side of vulval slit, lateral field absent. **Male.**

Labial region not offset, labial disc not elevated, lateral lips usually present. Stylet 16–20 µm long, basal knobs pyriform, offset. DGO = 2–7 µm. **J2.** L = 340–490 µm, hemizonid anterior or adjacent to excretory pore, tail = 33–49 µm, short hyaline region (4–7 µm), tail tip rounded.

Hosts: Cotton, pigeon pea, okra, tomato, sorghum, bulrush millet and grasses.

Distribution: Southern Africa.

Isozymes: Phenotype unknown.

Remarks: Restricted distribution in Africa.

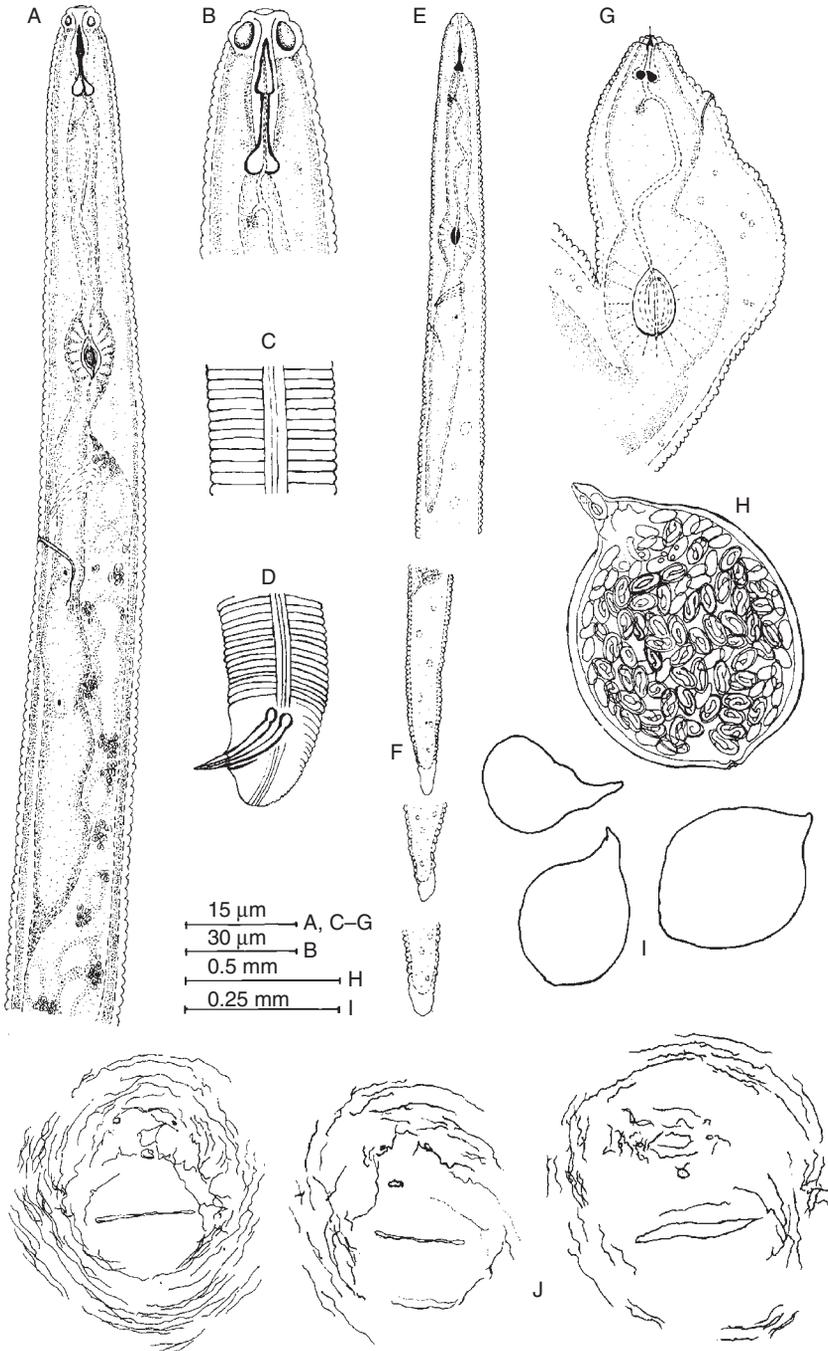


Fig. 3.13. *Meloidogyne acronea*. A: male pharyngeal region; B: male anterior region; C: male lateral field; D: male tail region; E: J2 pharyngeal region; F: J2 tail regions; G: female pharyngeal region; H: mature female; I: entire females; J: perineal patterns. After Page (1985), courtesy of CAB International.

3.6.6 *Meloidogyne chitwoodi* (Fig. 3.14)

Morphology: Female. Pear-shaped, with slight posterior protuberance. Stylet relatively small, 11–12.5 μm long, basal knobs small, rounded to irregularly shaped, posteriorly sloping. Several vesicle-like structures usually present within median bulb, clustered around lumen anterior to valve plates

of median bulb (Golden *et al.*, 1980). Perineal pattern rounded to oval, dorsal arch low and rounded to high and angular; striae near perineal area broken, curved, twisted; lateral lines weakly visible. **Male.** Labial region not offset, labial disc elevated, lateral lips present. Stylet 18–19 μm long, basal knobs small, irregularly shaped, posteriorly sloping, offset, DGO = 2.2–3.4 μm . **J2.** L = 336–417 μm ,

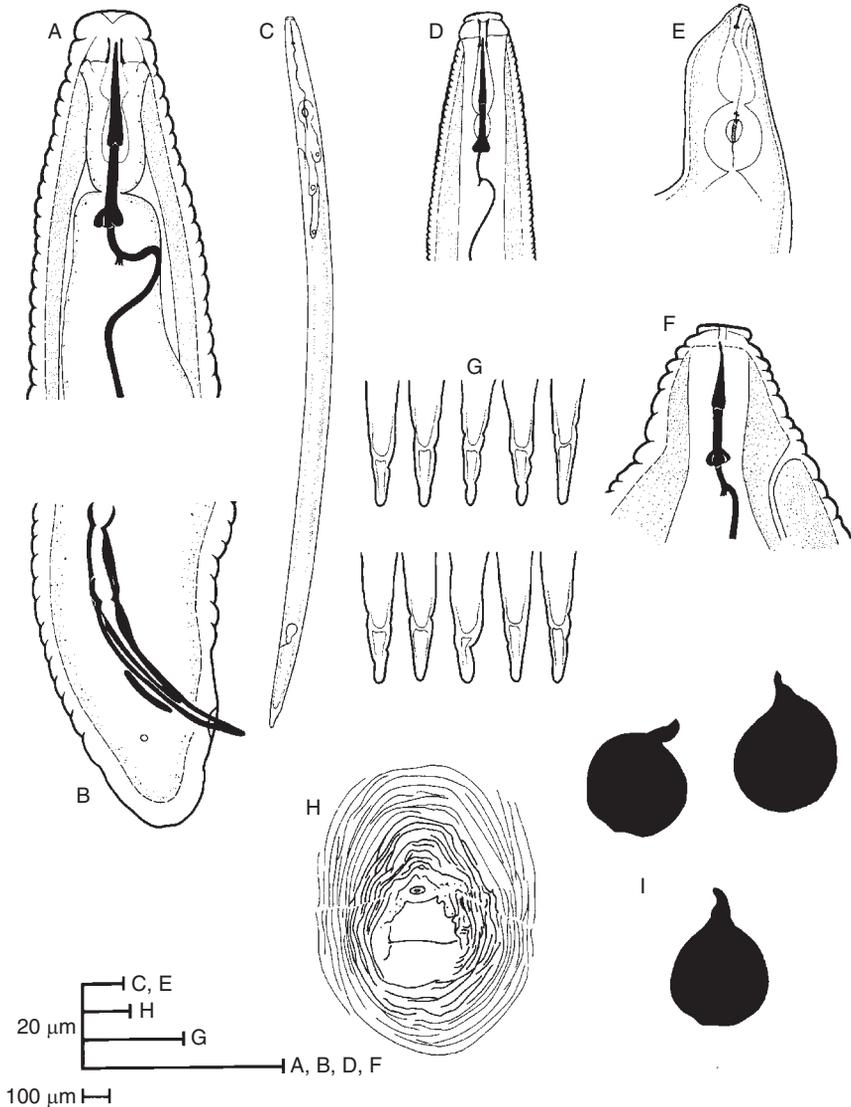


Fig. 3.14. *Meloidogyne chitwoodi*. A: male anterior region; B: male tail region; C: entire J2; D: J2 anterior region; E, F: female anterior region, lateral view; G: J2 tail regions; H: perineal pattern; I: entire females. After Jepson (1985), courtesy of CAB International.

hemizonid anterior or adjacent to excretory pore, tail = 39–47 µm with bluntly rounded tail tip and 9–14 µm long hyaline region.

Hosts: Potato and tomato are good hosts. Wide host range among several plant families, including crop plants and common weed species (barley, carrots, maize, sugarbeet, peas, wheat and various Poaceae). Attacking monocotyledons and dicotyledons.

Distribution: North America: Mexico, USA (California, Colorado, Idaho, Nevada, New Mexico, Oregon, Texas, Utah, Virginia, Washington). South America: Argentina. Europe: Belgium, Germany, The Netherlands, Portugal. Africa: South Africa.

Isozymes: The esterase phenotype is S1 and the malate dehydrogenase phenotype is N1a.

Remarks: Major species of economic importance attacking potato. Typically inciting galls similar to several other root-knot species, i.e. usually relatively small galls. Surface of infected potato tubers with numerous small, pimple-like, raised areas. It was added to the European list of quarantine organisms in 1998 to try to prevent further distribution within Europe.

3.6.7 *Meloidogyne enterolobii* (Fig. 3.15)

Morphology: **Female.** Pear-shaped, no posterior protuberance. Stylet 14–17 µm long, basal knobs reniform, indented, offset. Perineal pattern round to ovoid, dorsal arch rounded; striae fine, widely spaced; lateral field absent or with single line occurring at junction of dorsal and ventral arches. **Male.** Labial region not offset, labial disc not elevated, lateral lips absent. Stylet 18–25 µm long, basal knobs rounded, sloping posteriorly, offset, DGO = 3–5 µm. **J2.** L = 377–528 µm, hemizonid two annules anterior to excretory pore, tail = 43–63 µm with bluntly pointed tail tip and 5–15 µm long hyaline region.

Hosts: Aubergine, basil, bell pepper, coffee, soybean, sweet potato, tobacco, tomato, watermelon, guava, Spanish needle, bean, beet, broccoli, celery, horsebean, parsley, potato, pumpkin, American black nightshade, wild poinsettia, angel trumpet, glory bush, ajuga, glory flower.

Distribution: Brazil, China, Cuba, France, Guadeloupe, Malawi, Martinique, Puerto Rico, Senegal, South Africa, Switzerland, The Netherlands (intercept), Trinidad & Tobago, USA (Florida), Venezuela, West Africa (Ivory Coast and Burkina Faso).

Isozymes: Two major bands (VS1-S1 phenotype) of esterase activity and one strong malate dehydrogenase band (N1a).

Remarks: Widely distributed, emergent pest species with potential to cause great economic damage. Virulent on tomato cultivars with the *Mil* gene for resistance to other *Meloidogyne* spp. and on soybean cv. Forrest and sweet potatoes that are resistant to *M. incognita*. Damaging to coffee in Cuba and reproducing on tomato with *Mi* resistance gene. Typically inciting large, irregular galls. The nematode formerly known as *M. mayaguensis* is now regarded as a junior synonym of *M. enterolobii* (see Xu *et al.*, 2004 and EPPO, 2008).

3.6.8 *Meloidogyne ethiopica* (Fig. 3.16)

Morphology: **Female.** Elongate to pyriform, terminal protuberance absent. Stylet 12–15 µm long, basal knobs rounded, tapering gradually into shaft. Perineal pattern oval to squarish; dorsal arch moderately high to high; striae coarse, widely separated, smooth to wavy; lateral field indistinct. **Male.** Labial region not offset, labial disc distinct, lateral lips present. Stylet 23–27 µm long, basal knobs rounded to pear-shaped, offset. DGO = 3–5 µm. **J2.** L = 326–510 µm, hemizonid anterior to excretory pore, tail = 52–72 µm, hyaline region distinct (12–15 µm), tail tip finely rounded to pointed.

Hosts: Grapevine, kiwi, soybean and sugarcane.

Distribution: Mainly in East and Southern Africa and South America (Brazil, Chile) but also known from Slovenia.

Isozymes: The esterase phenotype E3 (Ki3) is species-specific and this is the most useful character for differentiating *M. ethiopica* from other species. Esterase phenotype (E3, Rm = 0.9, 1.05, 1.20); malate dehydrogenase N1 type.

Molecular: RAPD profiles were used by Carneiro *et al.* (2004a) to identify conspecific populations from Brazil, Chile and Kenya.

Remarks: Damaging species on grapevine and kiwi in South America (Brazil, Chile).

3.6.9 *Meloidogyne exigua* (Fig. 3.17)

Morphology: **Female.** Pear-shaped, no posterior terminal protuberance. Stylet 12–14 µm long, basal knobs rounded, offset. Perineal pattern

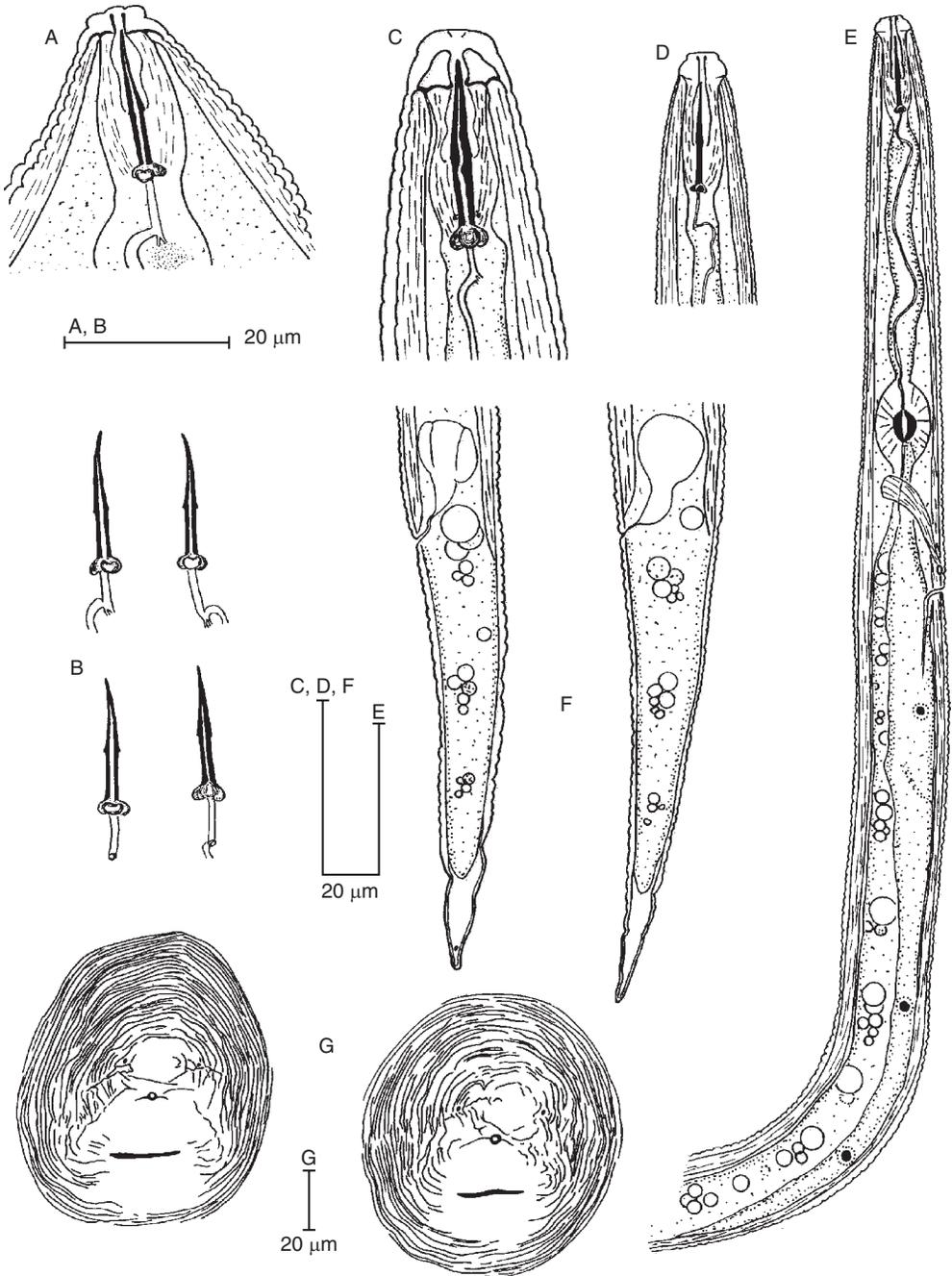


Fig. 3.15. *Meloidogyne enterolobii*. A: female anterior region; B: female stylets; C: male anterior region; D: J2 anterior region; E: J2 pharyngeal region; F: J2 tail regions; G: perineal patterns. After Rammah and Hirschmann (1988), courtesy of *Journal of Nematology*.

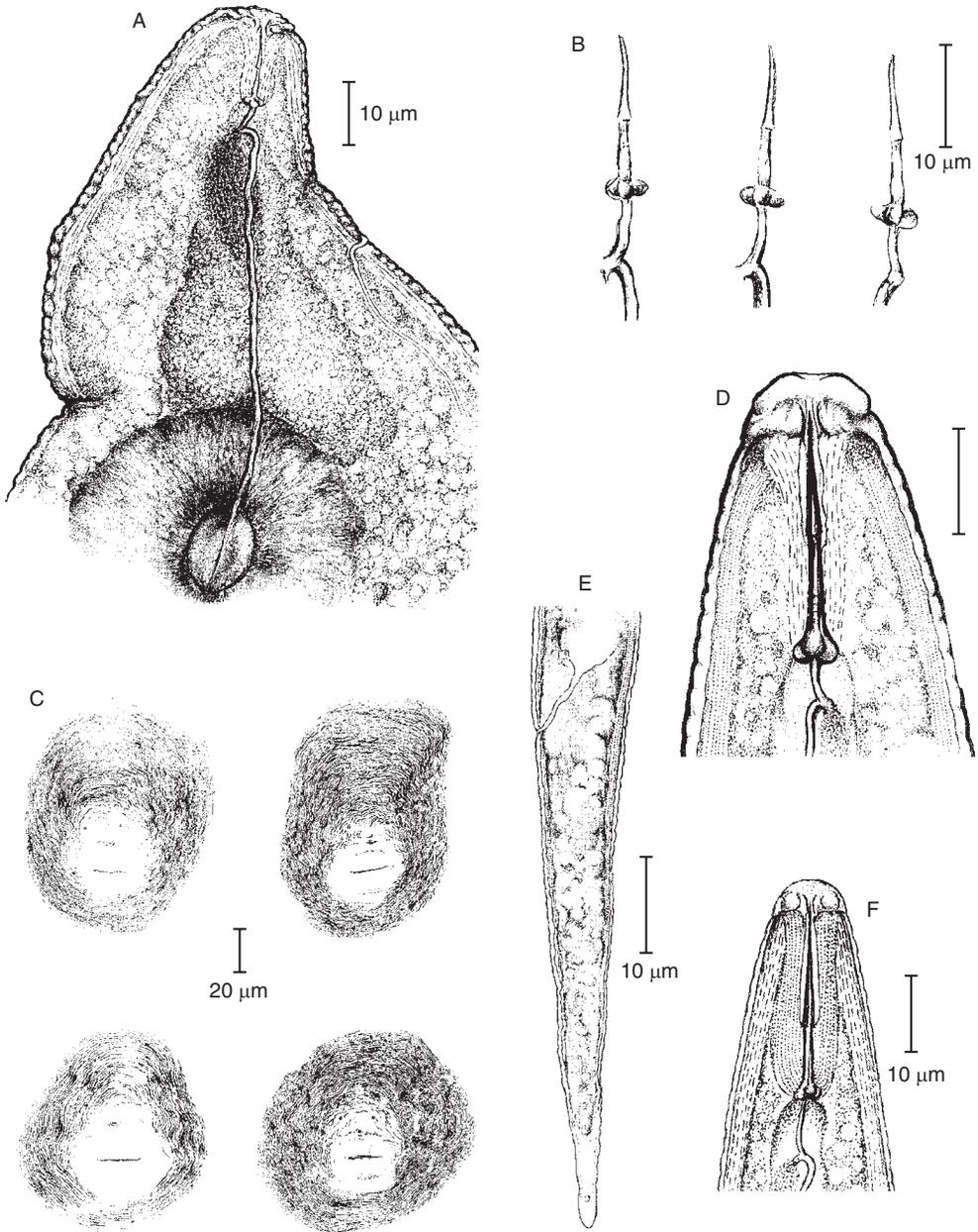


Fig. 3.16. *Meloidogyne ethiopica*. A: female pharyngeal region, lateral view; B: female stylets; C: perineal patterns; D: male labial region, lateral view; E: J2 tail, lateral view, F: J2 anterior region, lateral view. Modified after Carneiro *et al.* (2004a), courtesy of *Nematology*.

rounded/oval, low dorsal arch; striae smooth, widely spaced, coarse, broken and folded in lateral regions; lateral field absent. **Male.** Labial region slightly offset, with distinct elevated labial disc and one annule, lateral lips present, trapez-

oidal or almost triangular. Stylet 18–20 µm long, basal knobs rounded, posteriorly sloping, offset. DGO = 0.0–3.0 µm. **J2.** L = 290–370 µm, excretory pore opposite to posterior end of isthmus, tail = 39–50 µm with narrowly rounded tip.

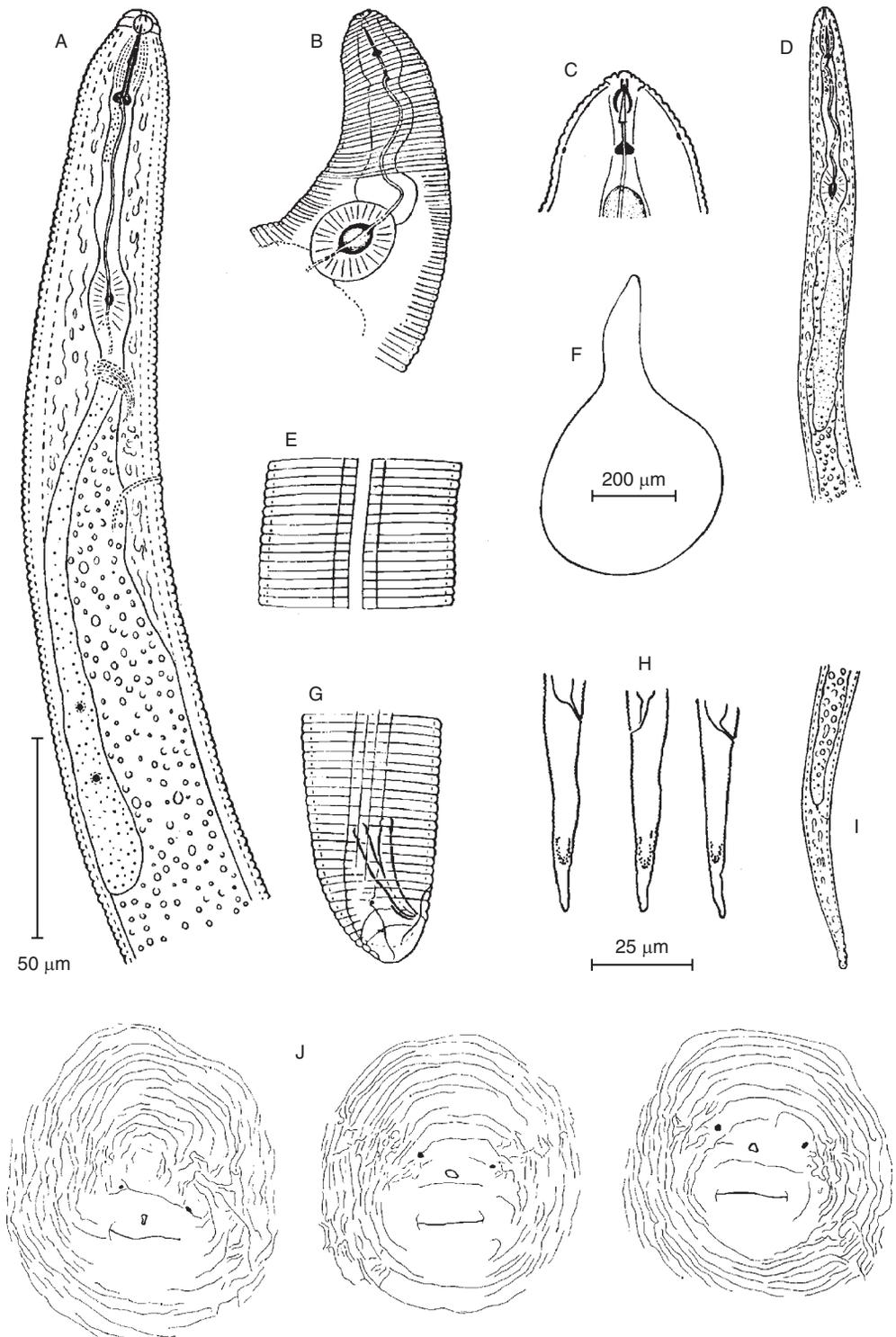


Fig. 3.17. *Meloidogyne exigua*. A: male pharyngeal region; B: female pharyngeal region; C: female anterior region; D: J2 pharyngeal region; E: male lateral field; F: entire female; G: male tail region; H, I: J2 tail regions; J: perineal patterns. A, B, D–G, after Lordello and Zamith (1958), courtesy of *Proceedings of the Helminthological Society of Washington*; C, H, after Whitehead (1968), courtesy of *Transactions of the Zoological Society of London*; J, courtesy of Janet Machon.

Hosts: Mostly attacking coffee, but also common weeds in coffee plantations. Fairly wide host range, including tomato, rice, sugarcane, banana, citrus, onion, etc. Race 3 attacks rubber trees (but not coffee) in Brazil.

Distribution: Widely distributed in humid coffee-producing areas of Central and South America. Occurs on coffee in Brazil, Guatemala, Peru, Suriname, Colombia, Venezuela, Costa Rica, El Salvador, Dominican Republic, Martinique. In Asia: India. Also found on other crops in Trinidad, French West Indies, China. In Europe: Greece, Italy.

Isozyme: The VF1 esterase phenotype of *M. exigua* is shared with *M. naasi*, although it can be differentiated from the latter by its N1 malate dehydrogenase phenotype.

Remarks: Attacks coffee in Central and South America. Outside this region it is a threat to all coffee-growing areas and is targeted in regulatory programmes. Typically inciting severe root galling in heavily attacked coffee and other plants.

3.6.10 *Meloidogyne fallax* (Fig. 3.18)

Morphology: **Female.** Globular to pear-shaped, with slight posterior protuberance. Stylet 14–15 μm long, basal knobs large, rounded to transversally ovoid, offset. One or two large and several smaller vesicle-like structures located along lumen lining. Perineal pattern ovoid to oval-shaped, or rectangular; dorsal arch low to moderately high, striae coarse; tail terminus and lateral field indistinct, resulting in a relatively large area without striae. **Male.** Labial region slightly offset, labial disc rounded, elevated, fused with medial lips, lateral lips present. Stylet 19–21 μm long, basal knobs offset, large rounded, DGO = 3–6 μm . **J2.** L = 381–435 μm , hemizonid at same level as excretory pore, tail = 46–56 μm with broadly rounded tail tip and 12–16 μm long hyaline region.

Hosts: Potato, tomato, oyster plant, carrot. Attacks both monocotyledons and dicotyledons.

Distribution: Australia; Europe (Belgium, France, Germany, The Netherlands); New Zealand.

Isozymes: Characterized by a unique malate dehydrogenase N1b phenotype and the lack of any major esterase band. All populations share this rare malate dehydrogenase phenotype and 'null'

esterase phenotype. Prolonged esterase staining (60 min) revealed a very weak, three-banded pattern named F3.

Remarks: Morphologically closely related to *M. chitwoodi* and a pest of potato and cereals in Europe. Typically inciting small galls. Infected potato tubers with blister-like or raised swellings on surface. It was added to the European list of quarantine organisms to try to prevent further distribution within Europe.

3.6.11 *Meloidogyne graminicola* (Fig. 3.19)

Morphology: **Female.** Elongate, slight terminal protuberance present. Stylet 12–15 μm long, basal knobs ovoid, offset. Perineal pattern rounded/oval, striae smooth, lateral field absent. **Male.** Labial region not offset, labial disc not elevated, lateral lips usually present. Stylet 15–20 μm long, basal knobs ovoid, offset. DGO = 3–4 μm . **J2.** L = 410–480 μm , hemizonid anterior or adjacent to excretory pore, tail = 60–80 μm , tail tip finely rounded.

Hosts: Rice and many grasses. Dicotyledonous weeds may also act as good hosts.

Distribution: Common in rice-growing areas.

Isozymes: Esterase VS1 phenotype with one slow band with a large drawn-out area of enzymatic activity (Esbenshade and Triantaphyllou, 1985a,b). The malate dehydrogenase N1a phenotype is similar to that of *M. chitwoodi* and *M. salasi*.

Remarks: Major species attacking rice. Typically incites large galls, often at the root tip, which may become hooked.

3.6.12 *Meloidogyne paranaensis* (Fig. 3.20)

Morphology: **Female.** Ovoid/pear-shaped, no posterior terminal protuberance. Stylet 15–17.5 μm long, basal knobs broad, offset. Perineal pattern rectangular to oval, high dorsal arch; striae fine/coarse, smooth/wavy, lateral field absent. **Male.** Labial region not offset, labial disc elevated, lateral lips absent. Stylet 20–27 μm long, basal knobs round to transversally elongate, offset, DGO = 3.5–5.0 μm . **J2.** L = 389–513 μm ,

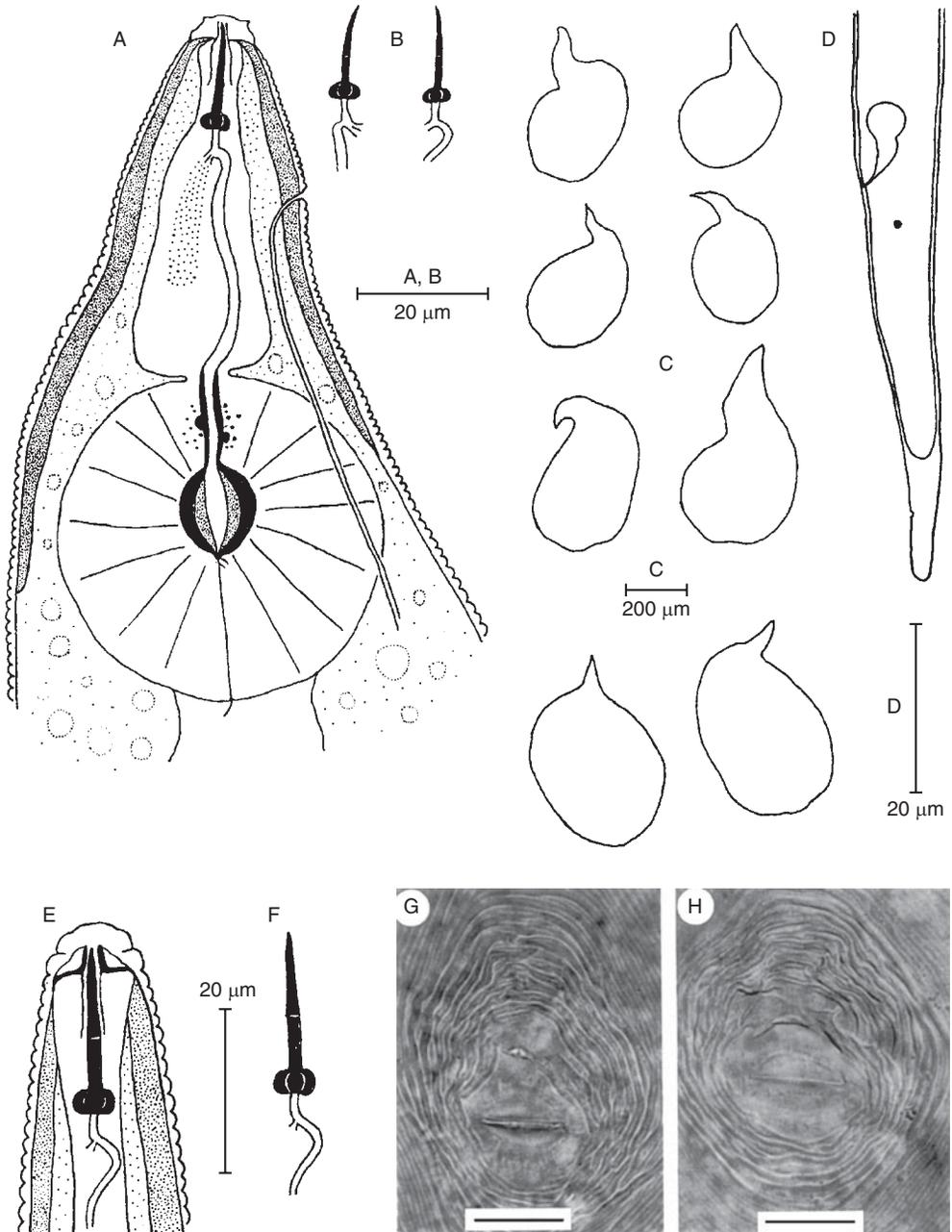


Fig. 3.18. *Meloidogyne fallax*. A: female pharyngeal region, lateral view; B: female stylets; C: entire females; D: J2 tail region, lateral view; E: male anterior region; F: male stylets; G, H: perineal patterns (scale bar = 25 μm). Modified after Karssen (1996), courtesy of *Fundamental and Applied Nematology*.

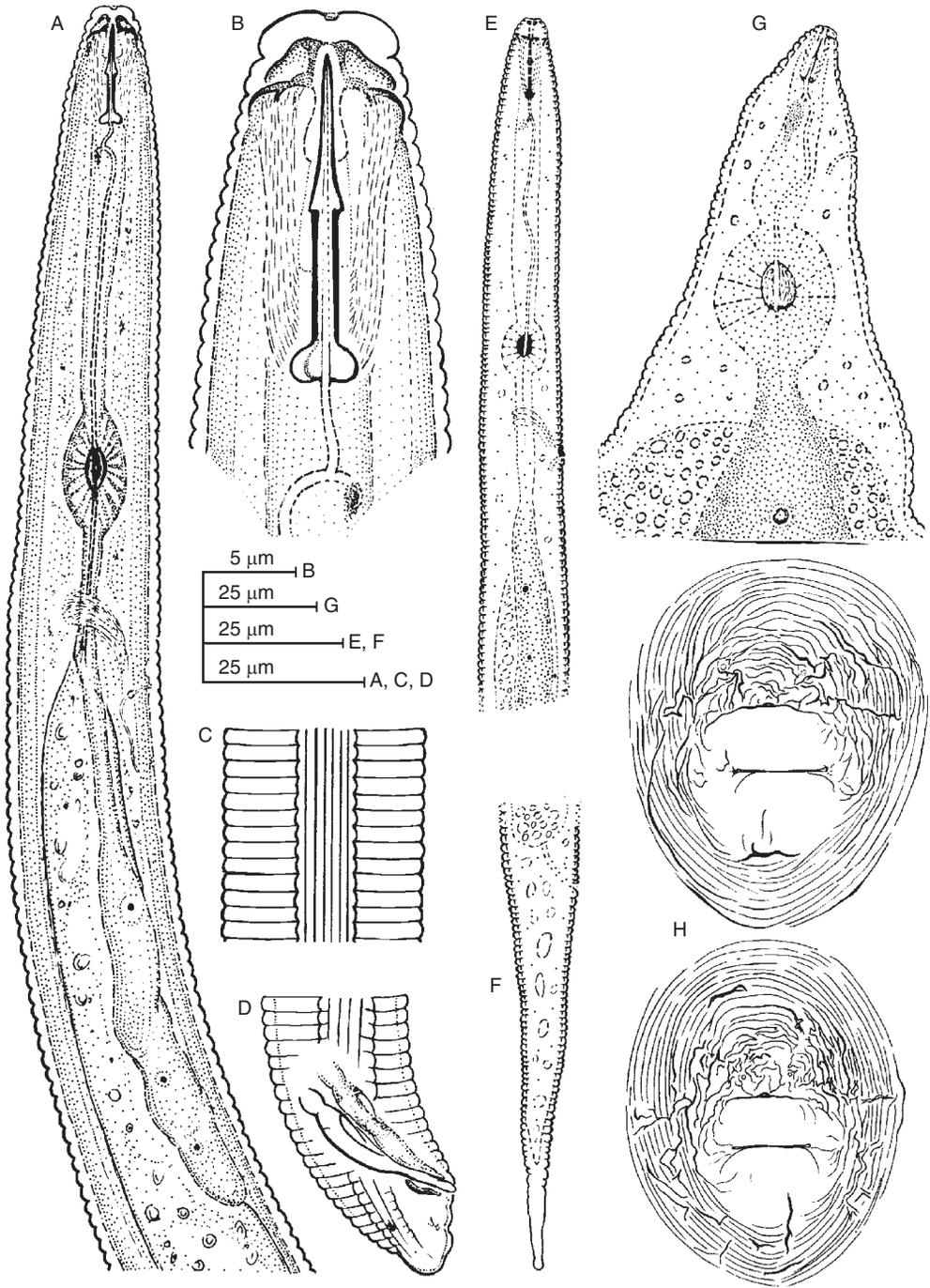


Fig. 3.19. *Meloidogyne graminicola*. A: male pharyngeal region; B: male anterior region; C: male lateral field; D: male tail region; E: J2 pharyngeal region; F: J2 tail region; G: female anterior region; H: perineal patterns. A–D, H, after Mulk (1976), courtesy of CAB International; E–G, after Golden and Birchfield (1965), courtesy of *Proceedings of the Helminthological Society of Washington*.

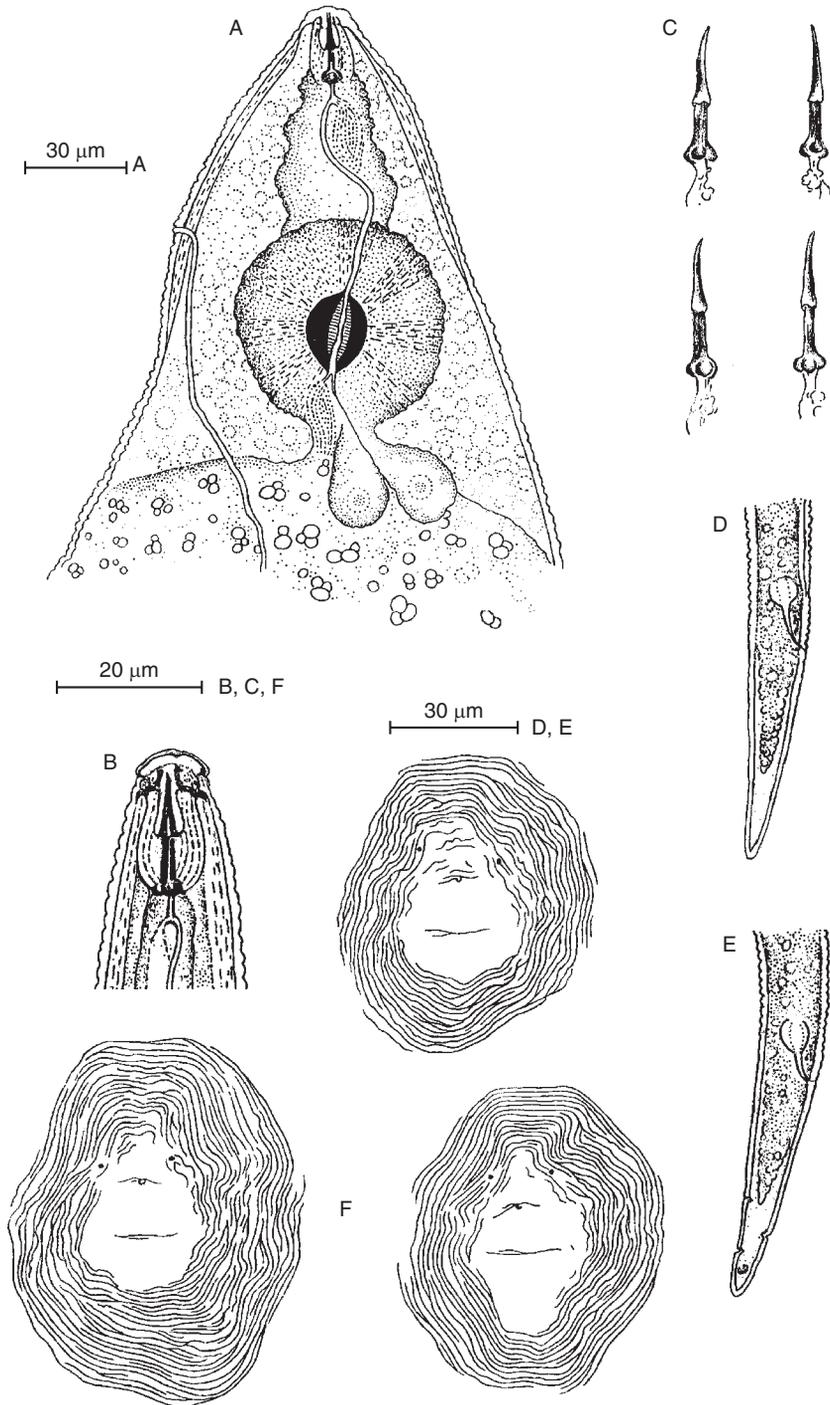


Fig. 3.20. *Meloidogyne paranaensis*. A: female pharyngeal region, lateral view; B: male anterior region, lateral view; C: female stylets; D, E: J2 tail region; F: perineal patterns. Modified after Carneiro *et al.* (1996), courtesy of *Journal of Nematology*.

hemizonid anterior to excretory pore, tail = 48–51 µm with rounded tail tip and 9–10 µm long hyaline region.

Hosts: Coffee, soybean. Also reproduces on tomato, tobacco, watermelon, mate (*Ilex paraguariensis*) and species of Solanaceae, Cucurbitaceae and Aquifoliaceae.

Distribution: Brazil, Guatemala.

Isozymes: The esterase phenotype has one fast-migrating band (F1) and the malate dehydrogenase phenotype is N1.

Remarks: Has potential to adversely affect threatened and endangered plant species. Symptoms include a cracking and splitting of the tap root of coffee but without gall formation.

3.7 Conclusions and Future Directions

There can be no doubt that there is a need for a minimum descriptive standard for any future proposals of new species in this genus. Such a protocol should take cognizance of the need for a blend of morphological (including SEM), morphometric, isozyme and molecular data. Naturally, opinion may vary as to which characters are essential and which are less so, yet still desirable, but with the genus rapidly approaching 100 'valid' species, the implementation of such a protocol cannot be long delayed if we are to avoid utter confusion in one of the most economically important groups of plant-parasitic nematodes. Carta *et al.* (2006) made certain recommendations in this regard, and in Eisenback and Hunt, Chapter 2, this volume, a protocol is

put forward which it is hoped will become widely accepted as a minimum standard.

The future prospects in root-knot nematode taxonomy and diagnostics are dependent on molecular-based methodologies that will discriminate not only at the species level but also at the level of host races, thereby opening up opportunities for more focused management strategies. Such techniques offer the possibility of rapid, unequivocal diagnostics and should help resolve the present problems associated with relatively morphologically conserved organisms that reproduce, for the most part, parthenogenetically. Once such techniques are widely employed no doubt a number of the current nominal species will be shown to be junior synonyms, while others, conversely, will be shown to be species complexes, possibly of sibling species. It seems likely that molecular methodologies will replace isozymes as the preferred diagnostic tool because of their inherently higher resolution and the opportunity to develop DNA chips for rapid and reliable field identification. Molecular characterization will also enhance our understanding of the phylogeny of the genus and its relationship with other plant-parasitic nematodes.

3.8 Acknowledgements

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